Subterranean Biology 48: 73–116 (2024)
doi: 10.3897/subtbiol.48.113383
https://subtbiol.pensoft.net

CHECKLIST

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

What`s crawling in the dark? An annotated list of gastropods in Greek caves

Danae Karakasi[1], Kaloust Paragamian[2], Moissis Mylonas[1], Katerina Vardinoyannis[1]

1 *Natural History Museum of Crete, School of Sciences and Engineering, University of Crete, Knossou Av., Heraklion, Crete, Greece* **2** *Hellenic Institute of Speleological Research, Megalou Alexandrou 179, Heraklion, Crete, Greece*

Corresponding author: Danae Karakasi (danae@nhmc.uoc.gr)

Academic editor: Ana Sofia P.S. Reboleira | Received 27 September 2023 | Accepted 30 January 2024 | Published 13 February 2024

https://zoobank.org/486102C9-EC73-4760-BF1C-196606EDF227

Citation: Karakasi D, Paragamian K, Mylonas M, Vardinoyannis K (2024) What`s crawling in the dark? An annotated list of gastropods in Greek caves. Subterranean Biology 48: 73–116. https://doi.org/10.3897/subtbiol.48.113383

Abstract

Greece is covered by a high percentage of carbonate rocks, resulting in a significant number of over 10,000 caves within its territory. Their fauna is not well known. Concerning gastropods, 68 terrestrial species have been reported from 70 caves. In this study, we contribute to the knowledge of the snails inhabiting Greek caves. We analyzed the literature and studied all the material deposited in the Natural History Museum of Crete, to create a first comprehensive list of gastropods of Greek caves. The number of caves from which gastropod species were reported increased to 182, while the number of known terrestrial species increased to 113. Fourteen of these species live only in caves, twelve of which are endemic of Greece. However, the fauna of Greek caves is still understudied. With the increasing exploration of Greek caves, the number of the known cave-dwelling gastropod species will increase and new species will be discovered.

Keywords

Biodiversity, cave fauna, gastropoda, Greece, snails

Introduction

Karst terrains and karstic processes are significant components of the physical geography of the Mediterranean basin. A substantial percentage of the land area of Greece is covered by carbonate rocks, where most caves are formed. According to Chen et al. (2017), approximately 41% of the land surface of Greece is characterised by the

Copyright *Danae Karakasi et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

presence of carbonate rocks. As a result, Greece, an area of 132,000 km^2, hosts more than 10,000 known caves (Beron 2016).

Among these caves, several hundred have been studied speleobiologically but faunistic data have been published only for 550. For terrestrial gastropods, 68 species have been reported from 70 caves (Paragamian et al. 2023). These species belong to 30 genera within 15 families, while half of them are Greek endemics (33/68). Fifty-nine of the species have been identified at species level; while 14 have been characterised as troglobionts, 30 as troglophiles and 15 as trogloxenes.

The classification of species living in subterranean environments has been a subject of debate [for a review, see Sket (2008, 2016) and Trajano and de Carvalho (2017)]. In this study, we refer to the terms of the Schiner-Racovitza's classification system, according to the lifestyle of the species as such: troglobiont, if a species lives exclusively in caves; troglophile, if it lives and reproduces in surface habitats but is also able to live and reproduce inside caves; trogloxene, if a species has an accidental presence in the cave or is considered an occasional visitor that does not live or reproduce in caves.

In this study, we contribute to the knowledge of the Greek cave gastropod fauna by presenting data from Greek caves based on the collections of the Natural History Museum of Crete (NHMC) and a thorough analysis of the literature.

Materials and methods

The present list is based on samples from caves in the collections of the NHMC and on the published data. The studied material is stored in the collections of the NHMC and consists of 96% ethanol-preserved specimens and dry material (empty shells). Most of the material was part of the collection of Kaloust Paragamian (KP, co-author) who donated his collection to the NHMC in 2018. It includes specimens from 137 caves and potholes (a single shaft, or an entire cave system that is dominantly vertical) that were collected between 1976 and 2019, mainly by KP but also by other Greek speleobiologists and cavers during their excursions (Fig. 1).

The majority of the specimens were identified at species level, following the taxonomy of MolluscaBase (2023). Where necessary, anatomical features of the reproductive system were also used for identification. In a few specimens, the anatomical characteristics were not clear due to preservation in 96% alcohol or the shells were broken. These specimens are reported at a genus level as *Genus* sp. or, if they resemble a specific species, they are reported as *Genus* aff. sp. (having affinity with but not identical to).

Additionally, we analysed the published data on cave-dwelling gastropods of Greece and included in the presented list all records reported as occurring in a cave. We excluded records, where it was uclear whether the species were collected inside or outside the cave (e.g. around the cave entrance).

For each species, we indicate the cave(s) in which it was found, based on the literature and the NHMC samples. The latter are reported as "present study". Note that if no other bibliographic references are given in a record, it is a new record for the Greek cave fauna.

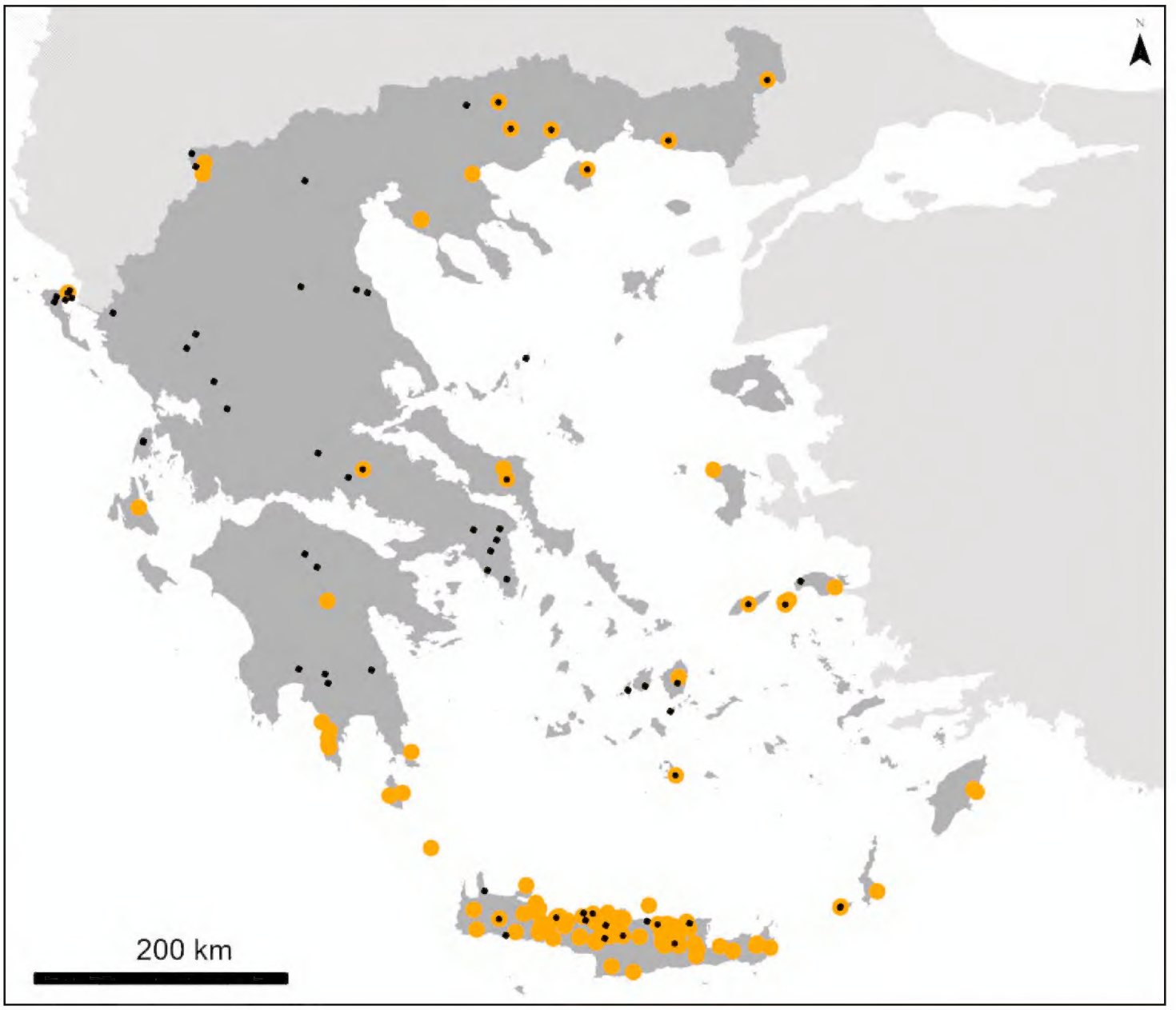

Figure 1. Caves in Greece with records of terrestrial gastropods from the literature (black dots) and from the present study (orange circles).

Sometimes the cave may have more than one name, in which case we follow the cave nomenclature of the Hellenic Institute of Speleological Research (Paragamian and Paragamian 2023), whereas the Greek letter transliteration is based on ELOT 743 standard.

The list is presented in alphabetical order of Order, Family, Genus and Species name. For each species, the cave(s) in which it is recorded, is given. The caves are presented in an alphabetical order of their TRADITIONAL GEOGRAPHIC REGION, Regional Unit and Cave name. However, for all islands, the island name is preferred to the Regional Unit, and they are divided into Aegean (including all islands of the Aegean Sea), Ionian (including all islands of the Ionian Sea) and Crete (including Crete island and its adjacent islets) areas (Fig. 2). The general distribution/endemism (Distribution), is also given for each species. Single-cave endemics, single-island endemics and stenoendemics (species with a few known localities within a very restricted area) are specifically mentioned. Finally, the ecological classification (Classification: Troglobiont, Troglophile, Trogloxene) and the published IUCN Red List category (IUCN 2023) are given for each species. The IUCN Red List categories are: Extinct (EX),

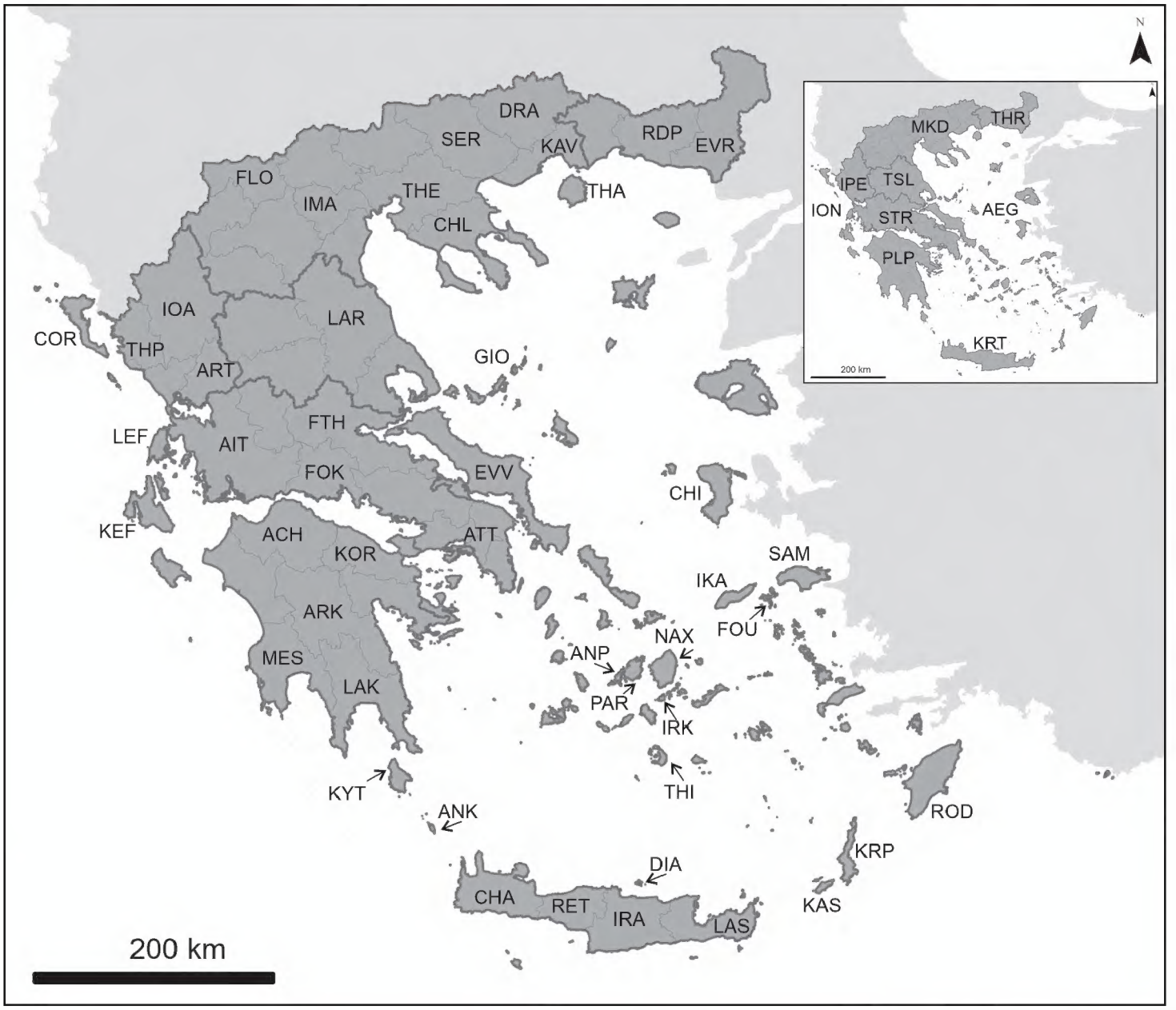

Figure 2. Map showing the Regional Units and Islands of Greece that are mentioned in the text. **Regional Units**: Achaia: **ACH**, Aitoloakarnania: **AIT**, Arkadia: **ARK**, Arta: **ART**, Attiki: **ATT**, Chalkidiki: **CHL**, Chania: **CHA**, Drama: **DRA**, Evros: **EVR**, Florina: **FLO**, Fokida: **FOK**, Fthiotida: **FTH**, Imathia: **IMA**, Ioannina: **IOA**, Irakleio: **IRA**, Kavala: **KAV**, Korinthia: **KOR**, Lakonia: **LAK**, Larisa: **LAR**, Lasithi: **LAS**, Messinia: **MES**, Rethymno: **RET**, Rodopi: **RDP**, Serres: **SER**, Thesprotia: **THP**, Thessaloniki: **THE**, Trikala: **TRI**. **Islands**: Antikythira: **ANK**, Antiparos: **ANP**, Chios: **CHI**, Corfu: **COR**, Dia: **DIA**, Evvoia: **EVV**, Fournoi: **FOU**, Gioura: **GIO**, Ikaria: **IKA**, Irakleia: **IRK**, Karpathos: **KRP**, Kasos: **KAS**, Kefalonia: **KEF**, Kythira: **KYT**, Lefkada: **LEF**, Naxos: **NAX**, Paros: **PAR**, Rodos: **ROD**, Samos: **SAM**, Thira: **THI**, Thasos: **THA**. Inset map showing the Traditional Geographic Regions of Greece. Aegean Islands: **AEG**, Crete: **KRT**, Ionian Islands: **ION**, Ipeiros: **IPE**, Makedonia: **MKD**, Peloponnisos: **PLP**, Sterea Ellada: **STR**, Thessalia: **TSL**, Thraki: **THR**.

Extinct In The Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) for evaluated species with adequate data, Data Deficient (DD) for evaluated species with inadequate data and Not Evaluated (NE) for not evaluated species. Detailed geographical information on the exact location of each cave is provided in Supplementary Material. The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, and are available at https://doi.org/10.15468/k57z2a.

Results

List of species in the caves of Greece

Terrestrial species

Phylum Mollusca
Class Gastropoda
Order Architaenioglossa
Family Cochlostomatidae
Genus *Cochlostoma*

***Cochlostoma cretense* (Maltzan, 1887)**

Distribution. Greek endemic, Crete (single-island endemic).
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Irakleio: Lakki Kontari Pothole (present study).

Family Cyclophoridae
Genus *Pholeoteras*

***Pholeoteras euthrix* Sturany, 1904**

Distribution. Western Balkan.
Classification. Troglobiont.
IUCN RedList. LC.
Records in Greek caves. Ionian: Corfu: Grava Tsouka Cave (Gittenberger 1977, 1985, 1986; Bernasconi and Riedel 1994; Štamol et al. 1999; Beron 2016; Paragamian et al. 2023).

Order Stylommatophora
Family Argnidae
Genus *Speleodentorcula*

***Speleodentorcula beroni* Gittenberger, 1985**

Distribution. Greek endemic, Evvoia-Peloponnisos.
Classification. Troglobiont.
IUCN RedList. VU.
Records in Greek caves. Aegean: Evvoia: Skoteini Cave (Gittenberger 1985; Beron 2016; Paragamian et al. 2023; present study).

Notes. The species was until recently known only from its type locality. A new subspecies, *S. beroni maniates* Reischütz, Steiner-Reischütz & Reischütz, 2017, was described from a site 250 kilometres southwest from its type locality by Reischütz et al. (2017). Further research is needed to clarify the taxonomy and distribution of this genus.

Family Azecidae
Genus *Hypnophila*

***Hypnophila zacynthia* (Roth, 1855)**

Distribution. Greek endemic, Ionian Islands-Opposite Greek mainland.
Classification. Troglophile.
IUCN RedList. LC.
Records in Greek caves. Ionian: Corfu: Katsouri Cave (Sturany 1904; Gittenberger 1977, 2000; Beron 2016; Paragamian et al. 2023).

Family Chondrinidae
Genus *Granopupa*

***Granopupa granum* (Draparnaud, 1801)**

Distribution. Mediterranean-Macaronesian-Turanian.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Lasithi: Pelekita Cave (present study).

Genus *Rupestrella*

***Rupestrella rhodia* (Roth, 1839)**

Distribution. Eastern Mediterranean.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Aegean: Rodos: Koumelou Cave (present study).

Family Clausiliidae
Genus *Albinaria*

***Albinaria contaminata* (Rossmässler, 1835)**

Distribution. Greece-Albania.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study).

Albinaria corrugata (Bruguière, 1792)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Irakleio: Agia Paraskevi Cave (Frank 1988; Paragamian et al. 2023; present study), Neraidospilios Cave (Frank 1988; Paragamian et al. 2023).

Albinaria discolor (Pfeiffer, 1846)

Distribution. Greek endemic, Aegean Islands-Sterea Ellada-Peloponnisos.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Aegean: Kythira: Katofygadi Cave (present study).

Albinaria eburnea (Pfeiffer, 1854)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Chania: Drakolaki Cave (present study).

Albinaria freytagi (Böttger, 1889)

Distribution. Greek endemic, Aegean Islands.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Votsos Agiou Charalampous Pothole, Megalos Votsos Panagias Pothole, Mikros Votsos Panagias Pothole (present study).

Albinaria grayana (Pfeiffer, 1846)

Distribution. Greek endemic, Aegean Islands-Peloponnisos.

Classification. Trogloxene.

IUCN RedList. NT.

Records in Greek caves. Aegean: Kythira: Niorou Cave (present study).

Albinaria munda (Rossmässler, 1836)

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Aegean: Samos: Vrysoulia Cave (present study).

***Albinaria senilis* (Rossmässler, 1836)**

Distribution. Greek endemic, Ionian Islands-Opposite Greek mainland.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study).

***Albinaria teres* (Olivier, 1801)**

Distribution. Greek endemic, Crete and adjacent islets.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Lasithi: Pelekita Cave (present study).

***Albinaria* sp.**

Records in Greek caves. Crete: Irakleio: Latsida sto Makry Lakki Pothole (present study).
Notes. The specimen could not be identified at species level because only a broken shell was collected, which belongs to a species of the genus *Albinaria*.

Genus *Carinigera*

***Carinigera buresi* (Wagner, 1928)**

Distribution. Greece-Bulgaria.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Kavala: Agia Eleni Cave; **Serres:** Alistrati Cave (present study).

Genus *Montenegrina*

***Montenegrina dofleini* (Wagner, 1928)**

Distribution. Western Balkan.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Florina: Panagia Eleousa Cave (Fehér and Szekeres 2016; Paragamian et al. 2023).

***Montenegrina sattmanni* Nordsieck, 1988**

Distribution. Greece-Albania-North Macedonia.

Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Florina: Kokkali Cave (Fehér and Szekeres 2016; Paragamian et al. 2023).

Genus *Sciocochlea*

***Sciocochlea collasi* (Sturany, 1904)**

Distribution. Greek endemic, Ionian Islands (single-cave endemic).
Classification. Troglobiont.
IUCN RedList. NT.
Records in Greek caves. Ionian: Corfu: Katsouri Cave (Sturany 1904; Wolf 1938; Gittenberger 1977, 1985, 1986, 2000; Beron 2016; Reischütz et al. 2016; Paragamian et al. 2023).

***Sciocochlea nordsiecki* Subai, 1993**

Distribution. Greece-Albania.
Classification. Troglobiont.
IUCN RedList. NT.
Records in Greek caves. Ipeiros: Thesprotia: Agios Neilos Cave (Subai 1993; Reischütz et al. 2016; Paragamian et al. 2023).
Notes. All known *Sciocochlea* material has been collected from deposits or debris originating from deep limestone crevices that are known, or thought to be, connected to caves. So far, no live specimens have been found (Reischütz et al. 2016).

Genus *Stigmatica*

***Stigmatica stigmatica* (Rossmässler, 1836)**

Distribution. Balkan-Italy.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study).

Genus *Tsoukatosia*

***Tsoukatosia christinae* Reischütz & Reischütz, 2003**

Distribution. Greek endemic, Peloponnisos (stenoendemic).
Classification. Troglobiont.
IUCN RedList. LC.

Records in Greek caves. Peloponnisos: Messinia: Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Reischütz et al. 2016, 2020; Paragamian et al. 2023).

Notes. No specimen of the genus *Tsoukatosia* has been recorded alive. The type locality of *T. christinae* is the indicated Agioi Anargyroi Cave, but empty shells have been recorded in other sites within coarse gravel. It is not known whether the species lives subterranean or in caves (Reischütz et al. 2020).

Family Enidae
Genus *Napaeopsis*

***Napaeopsis ossica* (Böttger, 1885)**

Distribution. Greek endemic, Makedonia-Thessalia.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Thessalia: Larisa: Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Bank and Menkhorst 1992; Paragamian et al. 2023).

Notes. All literature references are based on specimens from the Senckenberg Museum Frankfurt (SMF), but according to Bank and Menkhorst (1992) the specimens of *N. ossica* from this cave do no longer exist. The presence of this species from Kokkinos Vrachos Cave needs confirmation.

Genus *Rhabdoena*

***Rhabdoena cosensis* (Reeve, 1849)**

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Votsos sta Chalara Pothole (present study).

Genus *Mastus*

***Mastus sitiensis* Maassen, 1995**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Lasithi: Chonos Pothole (present study).

Genus *Zebrina*

***Zebrina detrita* (Müller, 1774)**

Distribution. European.
Classification. Trogloxene.
IUCN RedList. NE.
Records in Greek caves. Makedonia: Florina: Daoula Pothole; **Serres:** Alistrati Cave (present study). **Thessalia: Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Bank and Menkhorst 1992; Paragamian et al. 2023).

Family Ferussaciidae
Genus *Cecilioides*

***Cecilioides acicula* (Müller, 1774)**

Distribution. Euro-Mediterranean-Turanian-Macaronesian.
Classification. Troglophile.
IUCN RedList. LC.
Records in Greek caves. Aegean: Antikythira: Pano Spiliarida Cave; **Rodos:** Karolos Cave, Koumelou Cave (present study).

***Cecilioides michoniana* (Bourguignat, 1864)**

Distribution. Greece-Turkey.
Classification. Troglophile.
IUCN RedList. NE.
Records in Greek caves. Aegean: Rodos: Koumelou Cave (present study).

***Cecilioides tumulorum* (Bourguignat, 1856)**

Distribution. Mediterranean.
Classification. Troglophile.
IUCN RedList. LC.
Records in Greek caves. Aegean: Rodos: Koumelou Cave. **Crete: Lasithi:** Pelekita Cave, Theriospilios Cave. **Peloponnisos: Lakonia:** Agios Andreas Cave, Koukouri Cave; **Messinia:** Nerospiliako Cave (present study).

***Cecilioides* sp.**

Records in Greek caves. Ionian: Corfu: Kerkyra caves (Gittenberger 1977; Paragamian et al. 2023).

Family Gastrodontidae
Genus *Zonitoides*

***Zonitoides nitidus* (Müller, 1774)**

Distribution. Holarctic.
Classification. Troglophile.
IUCN RedList. NE.
Records in Greek caves. Makedonia: Imathia: Apano Skala Cave (Riedel 1959, 1992; Beron 2016; Paragamian et al. 2023).

Family Helicidae
Genus *Helix*

Helix* aff. *lucorum

Records in Greek caves. Thraki: Rodopi: Maroneia Cave (present study).

Genus *Cantareus*

***Cantareus apertus* (Born, 1778)**

Distribution. Mediterranean.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Irakleio: Arkalospilios Cave (present study).

Family Helicodontidae
Genus *Lindholmiola*

***Lindholmiola barbata* (Férussac, 1821)**

Distribution. Greek endemic, Crete and adjacent islets.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Chania: Achyrospilios Cave, Lentaka Trypa Cave (present study); **Rethymno**: Gerani Cave (Subai and Neubert 2014; Paragamian et al. 2023; present study).

***Lindholmiola corcyrensis* (Rossmässler, 1838)**

Distribution. Balkan.
Classification. Trogloxene.
IUCN RedList. LC.

Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study). **Ipeiros: Thesprotia:** Agios Neilos Cave (Subai and Neubert 2014; Paragamian et al. 2023).

***Lindholmiola lens* (Férussac, 1832)**

Distribution. Greece-W Turkey.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study). **Sterea Ellada: Fthiotida:** Mavri Troupa Cave (Subai and Neubert 2014; Paragamian et al. 2023). **Peloponnisos: Achaia**: Limnon Cave (Subai and Neubert 2014; Paragamian et al. 2023); **Arkadia:** Small caves near Agios Dimitrios (Subai and Neubert 2014; Paragamian et al. 2023); **Lakonia:** Agios Andreas Cave (present study).

***Lindholmiola spectabilis* Urbański, 1960**

Distribution. Greek endemic, Makedonia.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Makedonia: Serres: Alistrati Cave (present study).

Family Hygromiidae
Genus *Metafruticicola*

***Metafruticicola nicosiana* (Mousson, 1854)**

Distribution. Eastern Mediterranean.

Classification. Trogloxene.

IUCN RedList. DD.

Records in Greek caves. Crete: Chania: Amoutses Cave (present study).

***Metafruticicola noverca* (Pfeiffer, 1853)**

Distribution. Greek endemic, Aegean Islands and Crete

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Chania: Lentaka Trypa Cave, Metaxari Cave (present study).

***Metafruticicola redtenbacheri* (Pfeiffer, 1856)**

Distribution. Eastern Mediterranean.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Aegean: Chios: Agio Gala Cave; **Fournoi:** Votsos sta Chalara Pothole (present study).

***Metafruticicola sublecta* (Maltzan, 1884)**

Distribution. Greek endemic, Crete and adjacent islets.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Irakleio: Latsida sto Vathy Lakko I Pothole (present study).

Genus *Monacha*

***Monacha parumcincta* (Menke, 1828)**

Distribution. Balkan-Italy.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study).

Family Geomitridae
Genus *Xerocrassa*

***Xerocrassa* sp.**

Records in Greek caves. Aegean: Rodos: Koumelou Cave. **Crete: Lasithi:** Pelekita Cave (present study).

Genus *Xerolenta*

***Xerolenta obvia* (Menke, 1828)**

Distribution. European.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Serres: Alistrati Cave (present study).

Family Lauriidae
Genus *Lauria*

***Lauria cylindracea* (Da Costa, 1778)**

Distribution. Euro-Mediterranean-Turanian.

Classification. Trogloxene.
IUCN RedList. NE.
Records in Greek caves. Aegean: Fournoi: Megalos Votsos Panagias Pothole (present study).

Family Limacidae
Genus *Limacus*

***Limacus flavus* Linnaeus, 1758**

Distribution. Euro-Mediterranean.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Thraki: Rodopi: Maroneia Cave (present study).

Genus *Limax*

***Limax conemenosi* Böttger, 1882**

Distribution. Balkan.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Aegean: Samos: Panagia Spiliani Cave (present study).

***Limax graecus* Simroth, 1889**

Distribution. Balkan-Italy.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Chalkidiki: Nychteridon Cave; **Kavala:** Agia Eleni Cave; **Thraki: Rodopi:** Maroneia Cave (present study).
Notes. A slug was collected and identified as *Limax* aff. *graecus* in Petralona Cave (Makedonia: Chalkidiki) (present study).

***Limax* sp.**

Records in Greek caves. Crete: Irakleio: Afentis Christos Pothole (present study). **Ipeiros: Arta:** Trypa Rendes Cave (Beron 2016; Paragamian et al. 2023). **Sterea Ellada: Aitoloakarnania:** Gouva II Cave (Bonzano and Calandri 1984; Beron 2016; Paragamian et al. 2023)
Notes. Two species referred as *Limax maximus* var. *carbonaria* and *Limax maximus* var. *submaculata* are reported from **Thessalia: Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Paragamian et al. 2023). Their taxonomy is not clear and their presence has never been confirmed since their description.

Family Milacidae
Genus *Tandonia*

***Tandonia cretica* (Simroth, 1884)**

Distribution. Greek endemic, Greece.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Crete: Irakleio: Chamoto Spiliari Cave, Aspalathospilios Cave; **Lasithi**: Tafos Cave (present study).

***Tandonia totevi* (Wiktor, 1975)**

Distribution. Greece-Bulgaria.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Makedonia: Kavala: Agia Eleni Cave. **Thraki: Rodopi:** Maroneia Cave (present study).

***Tandonia* sp.**

Records in Greek caves. Crete: Chania: Kourna Cave; **Irakleio:** Latsida sto Vathy Lakko I Pothole, Latsida ston Gkremismeno Cave, Latsida tou Siganou Cave, Trachinolakka Pothole; **Rethymno:** Diplotafki Pothole, Gerani Cave, Profitis Ilias Cave, Sipouli Pothole; **Dia islet:** Petrokotsyfou Pothole (present study).

Family Oleacinidae
Genus *Poiretia*

***Poiretia compressa* (Mousson, 1859)**

Distribution. Greece-Albania.
Classification. Trogloxene.
IUCN RedList. LC.
Records in Greek caves. Ionian: Corfu: Anonymous cave at Pantokrator Mt. (Käufel 1930; Paragamian et al. 2023).

Family Orculidae
Genus *Orcula*

? *Orcula* sp.

Records in Greek caves. Aegean: Thira: Zoodochou Pigis Cave (Beron 2016; Paragamian et al. 2023).

Notes. This record needs confirmation, since the genus is absent from the Aegean islands. Most likely it is a misidentification.

Genus *Orculella*

***Orculella exaggerata* (Fuchs & Käufel, 1936)**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Kasos: Stylokamara Cave (Gittenberger and Hausdorf 2004; Paragamian et al. 2023).

***Orculella ignorata* Hausdorf, 1996**

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Votsos Agiou Theologou Pothole (present study).

***Orculella* sp.**

Records in Greek caves. Crete: Lasithi: Pelekita Cave (present study).

Notes. Only juvenilles collected. Around the cave, *Orculella cretiminuta* Gittenberger & Hausdorf, 2004 is present.

Family Oxychilidae
Genus *Carpathica*

***Carpathica cretica* (Forcart, 1950)**

Distribution. Eastern Mediterranean.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Irakleio: Agia Paraskevi Cave (present study); **Rethymno**: Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023).

***Carpathica insularis* Riedel & Mylonas, 1988**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Megalos Votsos Panagias Pothole (Riedel 1988a, Riedel 1992; Paragamian et al. 2023).

Genus *Daudebardia*

***Daudebardia brevipes* (Draparnaud, 1805)**

Distribution. European.

Classification. Trogloxene.

IUCN RedList. NE.

Records in Greek caves. Crete: Rethymno: Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023).

***Daudebardia rufa* (Draparnaud, 1805)**

Distribution. European.

Classification. Trogloxene.

IUCN RedList. NE.

Records in Greek caves. Aegean: Evvoia: Katavothra Pothole (present study). **Sterea Ellada: Attiki:** Panos Cave (Riedel 1978; Riedel 1992; Paragamian et al. 2023). **Crete: Chania:** Tzani Spilios Cave; **Irakleio:** Lakki Kontari Pothole (present study); **Rethymno:** Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023). **Peloponnisos: Arkadia:** Kapsia Cave (present study).

Genus *Eopolita*

***Eopolita protensa* (Férussac, 1832)**

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. Aegean: Rodos: Koufovouni Pothole, Koumelou Cave (present study). **Sterea Ellada: Attiki:** Nymfolyptou Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023), Rachi I Cave (Riedel 1959; Paragamian et al. 2023). **Crete: Chania:** Agia Sofia Cave (present study), Kolympari Cave (Riedel 1968; Beron 2016; Paragamian et al. 2023), Kourna Cave; **Irakleio:** Afentis Christos Pothole, Anonymous cave at Chersonisos, Anonymous Latsida of Geraki Pothole, Chainospilios Cave, Chamoto Spiliari Cave, Fragkadoni Cave, Karvounolakos Pothole, Lakki Kontari Pothole, Meires Trypa Cave, Palmeti Tafkos Pothole; **Lasithi:** Achnistra Cave (present study); **Rethymno:** Idaio Antro Cave (Riedel 1968; Paragamian et al. 2023), Mythia Kampathoura Pothole (present study).

Genus *Mediterranea*

***Mediterranea amaltheae* (Riedel & Subai, 1982)**

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. Crete: Irakleio: Faneromeni Cave, Latsida ston Gkremismeno Cave (present study); **Lasithi:** Diktaio Antro Cave (Riedel and Subai 1982; Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023, present study), Gaidourotrypa Cave, Peristeras Pothole, Tou Sfakianou i Trypa Pothole, Latsida Bempona Pothole (present study).

Notes. A remarkable extension of the distribution of *M. amaltheae* is reported. Until now, the species was known only from its type locality, Diktaio Antro Cave in Dikti Mt. (Lasithi, Crete). It is found in six other caves on the island and is therefore no longer a single-cave endemic but an island endemic.

***Mediterranea depressa* (Sterki, 1880)**

Distribution. Euro-Mediterranean.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Makedonia: Kavala: Agia Eleni Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023), Mavri Trypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023).

***Mediterranea hydatina* (Rossmässler, 1838)**

Distribution. European.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Antiparos: Antiparos Cave (Riedel 1983, 1992, 1996; Beron 2016; Paragamian et al. 2023); **Fournoi:** Votsos Agiou Charalampous Pothole (present study), Megalos Votsos Panagias Pothole (Riedel 1992, 1996; Paragamian et al. 2023; present study); **Ikaria:** Foutra Raos Cave (Martens 1889; Riedel 1983, 1992, 1996; Paragamian et al. 2023; present study); **Kasos:** Ellinokamara Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023); **Paros:** Kalampaki Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023); **Rodos:** Koufovouni Pothole (present study). **Crete: Chania:** Kolympari Cave (Riedel 1968, 1992; Beron 2016; Paragamian et al. 2023), Tzani Spilios Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Irakleio:** Afentis Christos Pothole, Latsida ston Gkremismeno Cave. **Makedonia: Florina:** Mikrolimni Cave (present study); **Serres:** Alistrati Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023; present study); **Thessaloniki:** Drakotrypa Cave (present study).

Mediterranea ionica (Riedel & Subai, 1978)

Distribution. Balkan-Italy.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Ionian: Corfu: Anonymous cave at Pantokrator Mt. (Käufel 1930; Riedel 1992, 1996; Paragamian et al. 2023), Katsouri Cave (Riedel 1978, 1992, 1996; Riedel and Subai 1982; Paragamian et al. 2023). **Ipeiros: Ioannina:** Anemotrypa Cave (Riedel 1992, 1996; Paragamian et al. 2023); **Thesprotia:** Agios Neilos Cave (Riedel and Subai 1993; Paragamian et al. 2023).

Mediterranea juliae (Riedel, 1990)

Distribution. Greece-Albania.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Ionian: Corfu: Megali Grava Cave (Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

Notes. Riedel and Subai (1993) reported this species from Agios Neilos Cave (Ipeiros, Thesprotia) but they note that its presence needs to be confirmed by anatomical data.

Mediterranea ? *mylonasi* (Riedel, 1983)

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Evvoia: Skoteini Cave (Riedel 1993, 1996; Beron 2016; Paragamian et al. 2023); **Gioura:** Kyklopa Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Samos:** Panagia Spiliani Cave (present study).

Notes. The taxonomy of the species is uncertain (Riedel 1992).

Mediterranea sp.

Records in Greek caves. Ipeiros: Ioannina: Platanousa Cave, (Klemm 1962 as *Oxychilus eudedaleus*; Riedel 1979, 1992 as *Oxychilus* (*Riedelius* ?) sp. (nova?); Beron 2016 as *Oxychilus* (*Riedelius*?) sp. (nova?); Paragamian et al. 2023 as *Oxychilus* sp.).

Genus *Morlina*

Morlina glabra (Rossmässler, 1835)

Distribution. European.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Evvoia: Katavothra Pothole (present study); **Thasos:** Drakotrypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023; present study). **Makedonia: Drama:** Maara Cave; **Florina:** Mikrolimni Cave (present study); **Imathia:** Apano Skala Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023); **Kavala:** Agia Eleni Cave (present study), Mavri Trypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023; present study); **Serres:** Pestereta Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023); **Thessaloniki:** Drakotrypa Cave (present study). **Thessalia: Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Riedel 1992; Beron 2016; Paragamian et al. 2023).

Genus *Oxychilus*

***Oxychilus cyprius* (Pfeiffer, 1847)**

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. Makedonia: Imathia: Apano Skala Cave (Riedel 1959, 1983, 1992; Beron 2016; Paragamian et al. 2023).

***Oxychilus seidli* Riedel, 1999**

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Votsos Agiou Charalampous Pothole, Megalos Votsos Panagias Pothole (present study).

***Oxychilus superfluus* (Pfeiffer, 1849)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Crete: Irakleio: Chainospilios Cave, Latsida sto Vathy Lakko I Pothole (present study); **Rethymno**: Idaio Antro Cave (Riedel 1968; Paragamian et al. 2023).

***Oxychilus* sp.**

Records in Greek caves. Sterea Ellada: Fokida Zoodochos Pigi Cave (Alexiou et al. 2014), Mayer Cave (Alexiou et al. 2014; Paragamian et al. 2023). **Crete: Chania**: Agia Sofia Cave (present study), Kolympari Cave as **?** *Oxychilus subeffusus* (Riedel

1968, 1992; Beron 2016; Paragamian et al. 2023); **Irakleio:** Stou Bokou ton Poro Pothole; **Rethymno**: Katerianos Tafkos Pothole (present study). **Peloponnisos**: **Messinia:** Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Genus *Schistophallus*

***Schistophallus minoicus* (Riedel, 1968)**

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Crete: Irakleio: Faneromeni Cave, Latsida sto Vathy Lakko I Pothole (present study); **Lasithi:** Diktaio Antro Cave (Riedel 1968, 1996; Maassen and Riedel 1991; Beron 2016; Paragamian et al. 2023, present study), Tou Sfakianou i Trypa Pothole (present study).

***Schistophallus samius* (Martens, 1889)**

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. Aegean: Chios: Agio Gala Cave (present study), Cave in Chios (Martens 1889); **Fournoi:** Megalos Votsos Panagias Pothole (Riedel 1993, 1996; Paragamian et al. 2023); **Naxos:** Za Cave (Beron 2016; Paragamian et al. 2023); **Samos:** Cave on Kerketeas Mt. (Martens 1889; Riedel 1958, 1972, 1992, 1996; Beron 2016; Paragamian et al. 2023), Panagia Spiliani Cave (present study). **Sterea Ellada: Attiki**: Vredou Cave (Riedel 1972; Beron 2016; Paragamian et al. 2023). **Peloponnisos: Achaia:** Limnon Cave (Riedel 1986, 1992, 1996; Beron 2016; Paragamian et al. 2023); **Lakonia:** Katafygi Cave (Anavryti) (Riedel 1992, 1996; Paragamian et al. 2023); **Korinthia:** Cave at Saitas Mt. (Arndt and Subai 2012).

***Schistophallus spratti* (Westerlund, 1892)**

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Crete: Chania: Amoutses Cave, Arapi Trypa Pothole, Kourna Cave, Lentaka Trypa Cave, Metaxari Cave (present study), Tzani Spilios Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Zoures Cave (present study); **Irakleio:** Kynigotafkos Pothole, Poros Stenou Lagkou Pothole, Stou Bokou ton Poro Pothole (present study); **Rethymno:** Afroimou Cave, Dolonas Cave (present study), Gerani Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023), Kaoudi Tafkos Pothole, Maryle Trypa Cave, Platani Cave, Tafkos Myristis Pothole, Tigania Cave, Voreini Trypa Cave, Skylogkremi Cave (present study).

Family Pagodulinidae
Genus *Pagodulina*

***Pagodulina* sp.**

Records in Greek caves. Peloponnisos: Messinia: Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Family Pleurodiscidae
Genus *Pleurodiscus*

***Pleurodiscus balmei* (Potiez & Michaud, 1838)**

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Megalos Votsos Panagias Pothole, Mikros Votsos Panagias Pothole; **Samos:** Panagia Spiliani Cave, Vrysoulia Cave (present study).

***Pleurodiscus sudensis* (Pfeiffer, 1846)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Crete: Irakleio: Chainospilios Cave, Chonos Sarchou Cave, Anonymous Latsida of Geraki Pothole, Chamoto Spiliari Cave, Fragkadoni Cave, Doxa Cave, Arkalospilios Cave, Faneromeni Cave, Karvounolakkos Cave, Karvounolakos Pothole, Lakki Kontari Pothole, Latsida of Moni Kaleri Pothole, Latsida sto Makry Lakki Pothole, Megalos Tafkos Pothole, Moni Kaleri Cave, Palmeti Tafkos Pothole, Peristerotafkos Pothole, Skararolithos Pothole, Stravomyti Cave, Trachinolakka Pothole, Xerakolagoufo Pothole; **Lasithi:** Trapeza Cave; **Rethymno:** Alykes Cave, Gerani Cave, Kamariti Cave, Karafti Tafkos Pothole, Katerianos Tafkos Pothole, Melidoni Cave, Peiraton Cave, Porou Trypa Cave, Skoteinospilios Cave, Stin Koryfi tis Viglas Pothole, Tafkos sti Gonia Pothole, Tafkos stin Pode Faragka Pothole, Trypiti Cave, Xepatomenos Tafkos Pothole (present study).

Family Pomatiidae
Genus *Pomatias*

***Pomatias elegans* (Müller, 1774)**

Distribution. Euro-Mediterranean.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Ionian: Kefalonia: Melissani Cave (present study).

Family Pristilomatidae
Genus *Gyralina*

***Gyralina formosa* Riedel & Subai, 1993**

Distribution. Greek endemic, Ipeiros (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. Ipeiros: Thesprotia: Agios Neilos Cave (Riedel and Subai 1993).

Notes. The shells were found in rock debris, on limestone rocks in the small cave chapel (Riedel and Subai 1993). In the type locality the species is known from 10 empty shells, including 7 adults, some very fresh. The species may also occur in other subterranean environments other than caves (unpublished data). If this is confirmed, then the species should be considered as a subterranean, troglophilous species.

***Gyralina tsatsae* Gittenberger, 1977**

Distribution. Greek endemic, Ionian Islands (single-island endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. Ionian: Corfu: Anthropograva Cave (Gittenberger 1977; Riedel 1992; Beron 2016; Paragamian et al. 2023), Grava Tsouka Cave (Gittenberger 1977; Riedel 1992; Beron 2016; Paragamian et al. 2023).

Genus *Lindbergia*

***Lindbergia beroni* Riedel, 1984**

Distribution. Greek endemic, Aegean Islands (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. Aegean: Thira: Zoodochou Pigis Cave (Riedel 1984, 1992, 1996; Beron 1985, 2016; Di Russo and Rampini 2001; Gasparo 2009; Paragamian et al. 2023; present study).

Notes. In the collections of the NHMC there are specimens of *Lindbergia* aff. *beroni* from Kanavari Cave (Aegean: Naxos).

***Lindbergia* ? *gittenbergeri* Pintér & Riedel, 1983**

Distribution. Greek endemic, Ionian Islands (single-island endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. Ionian: Corfu: Megali Grava Cave (Pintér and Riedel 1983; Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023), Anonymous cave (Riedel 1992; Beron 2016; Paragamian et al. 2023).

Notes. The presence of the genus on the island of Corfu requires confirmation (Riedel 1992).

Lindbergia aff. *karainensis*

Records in Greek caves. Aegean: Karpathos: Diaolospilios Cave (present study).

Lindbergia orbicularis (Riedel, 1962)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Crete: Chania: Agia Roumeli Cave (Riedel 1992, 1996; Paragamian et al. 2023), Metaxari Cave (present study), Tzani Spilios Cave (Riedel 1993, 1996; Beron 2016; Paragamian et al. 2023; present study); **Irakleio:** Agio Pnevma Cave, Anonymous Latsida of Geraki Pothole (present study), Chainospilios Cave (Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Doxa Cave, Karvounolakkos Cave, Lakki Kontari Pothole, Peristerotafkos Pothole, Schistra Cave, Skararolithos Pothole, Stou Bokou ton Poro Pothole, Trachinolakka Pothole, Xerakolagoufo Pothole (present study); **Lasithi:** Achnistres Cave, Peristera Cave (Agios Georgios), Peristera Cave (Vrachasi), Tafos Cave, Xepatomeni Latsida Pothole (present study); **Rethymno:** Chomatotafkos Pothole, Diplotafki Pothole, Erfoi Cave (present study), Gerani Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023), Kakalonia Pothole, Kamariti Cave, Karafti Tafkos Pothole, Katerianos Tafkos Pothole (present study), Melidoni Cave (Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023), Porou Trypa Cave, Tafkos stin Pode Faragka Pothole, Xanthou Cave, Xylouri Tafkos Pothole (present study).

Lindbergia ? *pageti* Riedel, 1968

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. Crete: Chania: Kolympari Cave (Riedel 1968, 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023).

Notes. Previously, the species was reported with certainty only from the type locality—Kolympari Cave—and was considered to be a troglobiont. Specimens from other locations in Crete and its adjacent islands have been reported in the past but their identification was uncertain and therefore not confirmed by Riedel (1992). The collection

of the NHMC has a lot more material than the material Riedel had the opportunity to study and as a result, Mylonas was able to confirm the presence of the species in other localities on Crete island and Western Paximadi islet. A specimen from Tafos Cave (Crete: Lasithi), most probably belongs to this species, *Lindbergia* aff. *pageti.* Research on the taxonomy of the species is still needed, as there are no anatomical data to confirm the genus.

Lindbergia pinteri Riedel, 1981

Distribution. Greek endemic, Aegean Islands (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. Aegean: Ikaria: Foutra Raos Cave (Riedel 1981a, 1992, 1996; Beron 2016; Paragamian et al. 2023).

Lindbergia pseudoillyrica Riedel, 1960

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Crete: Chania: Tzani Spilios Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Irakleio:** Achnistra Cave, Afentis Christos Pothole (present study), Agia Paraskevi Cave (Riedel 1960, 1968,1992, 1996; Beron 2016; Paragamian et al. 2023), Chonos Sarchou Cave (Riedel 1960, 1968, 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Meires Trypa Cave (present study); **Lasithi:** Agios Stavros Cave (present study), Diktaio Antro Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023), Theriospilios Cave (present study); **Rethymno:** Peristere Cave (ancient quarry)(Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023), Prinos Cave (Beron 2016; Paragamian et al. 2023), Sfentoni Trypa Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023).

Lindbergia spiliaenymphis Riedel, 1959

Distribution. Greek endemic, Sterea Ellada (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. Sterea Ellada: Attiki: Keratea Cave (Riedel 1959, 1960, 1968, 1977, 1992, 1996; Pintér and Riedel 1983; Beron 2016; Paragamian et al. 2023).

Lindbergia stylokamarae Riedel, 1981

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. Aegean: Kasos: Stylokamara Cave (Riedel 1981a, 1992; Beron 2016; Paragamian et al. 2023; present study).

***Lindbergia* sp.**

Records in Greek caves. Aegean: Irakleia: Agios Ioannis Cave, as *Lindbergia* sp. (nova) aff. *pseudoillyrica* (Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023). **Peloponnisos: Messinia:** Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Genus *Vitrea*

***Vitrea clessini* (Hesse, 1882)**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Kasos: Ellinokamara Cave (present study).

***Vitrea contracta* (Westerlund, 1871)**

Distribution. Euro-Mediterranean-Turanian-Macaronesian.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Megalos Votsos Panagias Pothole (Riedel 1992; Paragamian et al. 2023), Votsos Agiou Charalampous Pothole (Riedel 1992). **Crete: Lasithi:** Diktaio Antro Cave (Riedel 1992; Paragamian et al. 2023); **Rethymno:** Erfoi Cave (present study), Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023). **Peloponnisos: Lakonia:** Agios Andreas Cave (present study), Kaiadas Cave (Riedel 1992; Paragamian et al. 2023).

***Vitrea klemmi* Pintér, 1972**

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Ikaria: Foutra Raos Cave (Riedel 1981a, 1981b, 1992; Beron 2016; Paragamian et al. 2023).

***Vitrea neglecta* Damjanov & Pintér, 1969**

Distribution. Greece-Bulgaria-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Makedonia: Drama: Maara Cave (Georgiev 2016; Paragamian et al. 2023).

Vitrea ossaea Pintér, 1983

Distribution. Greek endemic, Thessalia (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. DD.

Records in Greek caves. Thessalia: Larisa: Profitis Ilias Cave (Pintér 1983; Riedel 1992; Riedel 1996; Beron 2016; Paragamian et al. 2023).

Notes. This species has also been reported from Peristera islet (Aegean) but the taxonomy of the specimen requires confirmation (Riedel 1992).

Vitrea riedeli Damjanov & Pintér, 1969

Distribution. Greece-Bulgaria-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Fournoi: Megalos Votsos Panagias Pothole (Riedel 1992; Paragamian et al. 2023; present study).

Vitrea riedeliana Paget, 1976

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Aegean: Rodos: Koufovouni Pothole, Koumelou Cave (present study).

Vitrea schuetti Pintér, 1972

Distribution. Greek endemic, Greece.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Sterea Ellada: Attiki: Ntavelis Cave (Pintér 1972; Riedel 1992; Beron 2016; Paragamian et al. 2023).

Vitrea subrimata (Reinhardt, 1871)

Distribution. Euro-Mahrebian.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Ipeiros: Thesprotia: Agios Neilos Cave (Riedel and Subai 1993).

Family Zonitidae
Genus *Allaegopis*

***Allaegopis jonicus* (Käufel, 1930)**

Distribution. Greek endemic, Ionian Islands-Opposite Greek mainland.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. Ionian: Lefkada: Egklouvi Cave (Käufel 1930; Riedel 1982, 1992; Beron 2016; Paragamian et al. 2023), Poly Trypes Cave (Käufel 1930; Riedel 1992; Paragamian et al. 2023).

Genus *Balcanodiscus*

***Balcanodiscus beroni* Riedel, 1995**

Distribution. Greek endemic, Makedonia (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. NT.

Records in Greek caves. Makedonia: Drama: Maara Cave (Riedel 1995, 1996; Beron 2016; Paragamian et al. 2023).

Notes. In the studies of Riedel (1995) and Beron (2016), the species is reported from two caves, Maara I and Maara II. These are not two different caves, but part of the same cave system called Maara.

***Balcanodiscus cerberus* Riedel, 1985**

Distribution. Greek endemic, Thraki (stenoendemic).

Classification. Troglophile.

IUCN RedList. NT.

Records in Greek caves. Thraki: Rodopi: Maroneia Cave (Riedel 1985b, 1988b, 1992, 1996; Reischütz 1986, 1988; Paragamian et al. 2004, 2023; Beron et al. 2004; Erőss et al. 2011; Beron 2016; present study).

***Balcanodiscus difficilis* Riedel, 1988**

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. NT.

Records in Greek caves. Aegean: Thasos: Drakotrypa Cave (Riedel 1988b, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

***Balcanodiscus frivaldskyanus* (Rossmässler, 1842)**

Distribution. Eastern Balkan.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. Thraki: Evros: Koufovouno Cave (Riedel 1969, 1985b, 1988b, 1992, 1996; Beron et al. 2004; Beron 2016; Paragamian et al. 2023; present study).

***Balcanodiscus* sp.**

Records in Greek caves. Makedonia: Serres: Alistrati Cave (Beron 2016; Paragamian et al. 2023).

Genus *Doraegopis*

***Doraegopis subaii* Riedel, 1990**

Distribution. Greek endemic, Sterea Ellada (stenoendemic).

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. Sterea Ellada: Fthiotida: Mavri Troupa Cave (Bank and Menkhorst 1988; Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

***Doraegopis* sp.**

Records in Greek caves. Peloponnisos: Achaia: Limnon Cave (Riedel 1982, 1986, 1992; Bank and Menkhorst 1988; Beron 2016; Paragamian et al. 2023).

Genus *Zonites*

***Zonites casius* Martens, 1889**

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Trogloxene.

IUCN RedList. NT.

Records in Greek caves. Aegean: Kasos: Stylokamara Cave (Riedel 1985a).

***Zonites nikariae* Pfeffer, 1930**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.
IUCN RedList. VU.
Records in Greek caves. Aegean: Ikaria: Foutra Raos Cave (Martens 1889; Riedel 1985a, 1992; Beron 2016; Paragamian et al. 2023).

Among the 113 species, 15 were not identified at the species level, i.e. *Pagodulina* sp., and were therefore excluded from any cave-dwelling category. The remaining 98 species include 14 troglobionts (14%), 39 troglophiles (40%) and 45 (46%) troglox-enes (Fig. 3). The percentage of troglobiont gastropods is lower than the total percent-age of troglobionts in the cave fauna in Greece (22.2%) (Paragamian et al. 2023). The troglobiont gastropods belong to eight genera, namely *Balcanodiscus* (1 species) (Zonitidae), *Gyralina* (2 species), *Lindbergia* (4 species), *Vitrea* (1species) (Pristiloma-tidae), *Mediterranea* (1 species) (Oxychilidae), *Pholeoteras* (1 species) (Cyclophoridae), *Sciocochlea* (2 species), *Tsoukatosia* (1 species) (Clausiliidae) and *Speleodentorcula* (1 spe-cies—monotypic genus) (Argnidae). All but two species (*Pholeoteras euthrix* and *Tsouk-atosia christinae*) are endemic to Greece and are listed as Threatened or Near Threatened in the IUCN Red List (2023) but none is legally protected. It is interesting to note that five of the endemic species are distributed on the mainland while the remaining eight are found on islands (Fig. 4). In particular, Corfu, an Ionian island, hosts four troglobiont species belonging to four genera, three of which are endemic to the island.

Almost half of the cave-dwelling gastropod species (49%), are endemic to Greece, which is close to the endemism percentage of the entire cave fauna of Greece, which is 45% (Paragamian et al. 2023). Many of these have a very restricted distribution, with twelve species being single-island endemics, and seven being single-cave endemics (Fig. 5).

The island of Crete is the most studied region of Greece, containing 55% of the explored caves. Mainland Greece and most of the Aegean and Ionian islands have not been intensively explored (Fig. 1). The reason for this difference in between regions is mostly a matter of sampling bias rather than the presence or absence of caves.

The maximum number of species reported in a cave—nine species—is recorded in two caves: Gerani Cave in Crete and Megalos Votsos Panagias Pothole in Fournoi. The majority of the caves (101) are reported to host only one species while 60 caves host 2–3 species and the remaining 19 host 4–7 species (Fig. 6).

Discussion and conclusions

In this study, 113 terrestrial gastropod species are reported from 182 Greek caves, thereby doubling the number of known cave-dwelling species and providing first records for 113 caves. The species belong to 49 genera within 23 families. The most species- and genus-rich families are Oxychilidae (19 species, 7 genera), Pristilomatidae (19 species, 3 genera), Clausiliidae (16 species, 6 genera) and Zonitidae (8 species, 4 genera). These, with the exception of Clausiliidae, are the most diverse subterranean families worldwide (Grego 2022) while all of them are among the most species-rich families in Greece with Clausillidae being the most speciose family in Greece (Vardinoyannis et al. 2018).

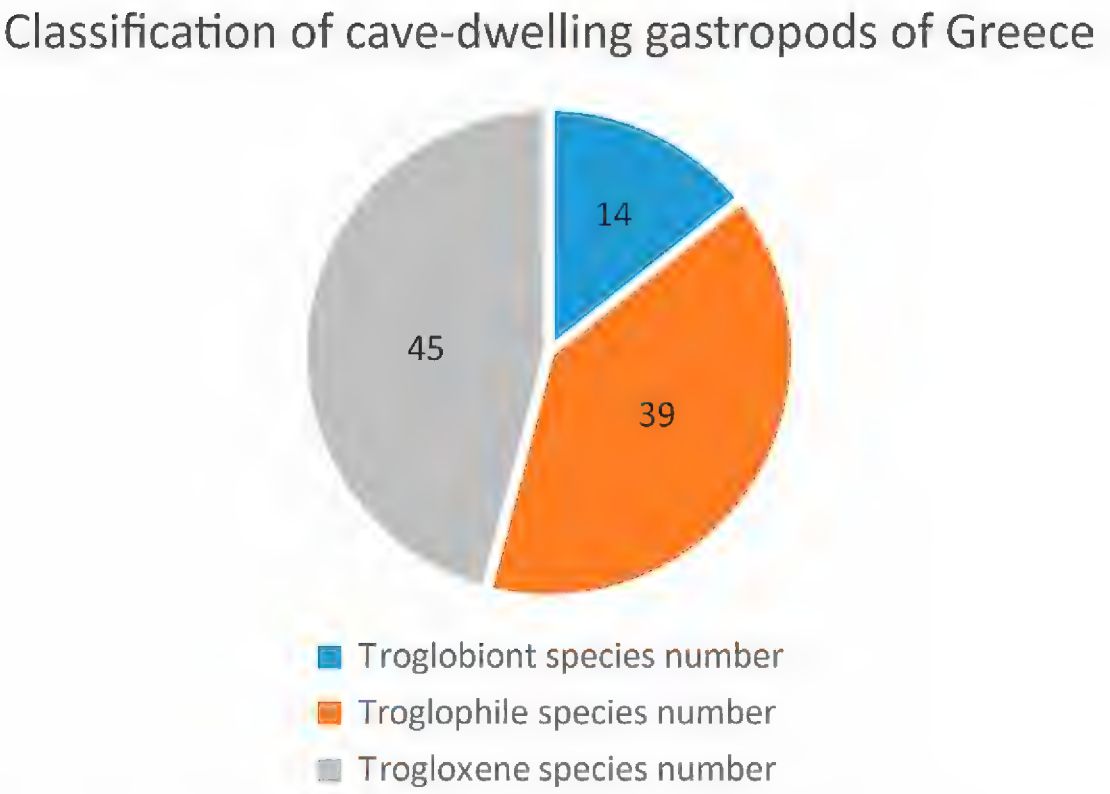

Figure 3. Ecological classification of the cave-dwelling gastropods in Greek caves.

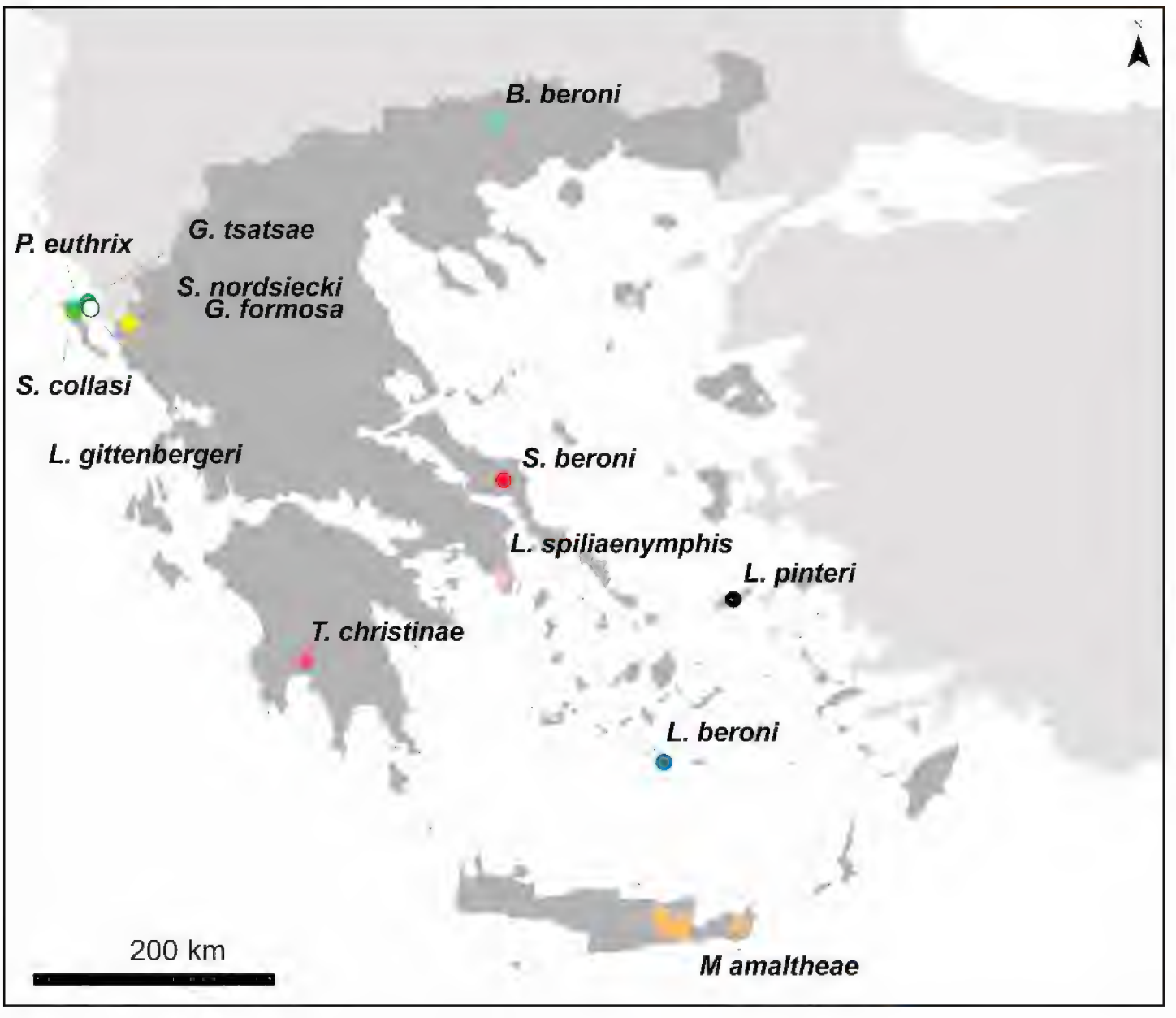

Figure 4. Troglobiont gastropod species of Greece.

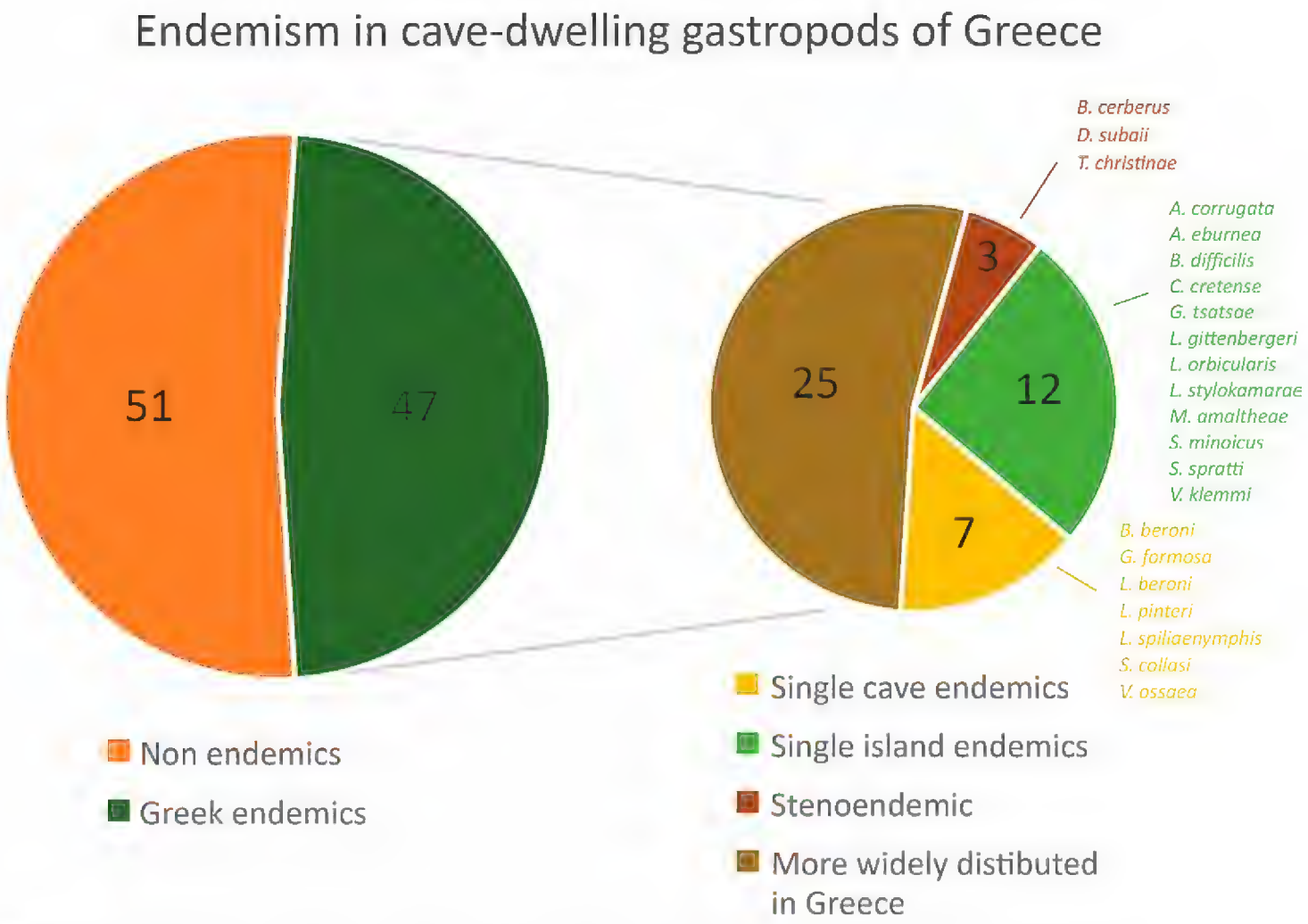

Figure 5. Number of endemic and non-endemic cave-dwelling gastropods in Greek caves.

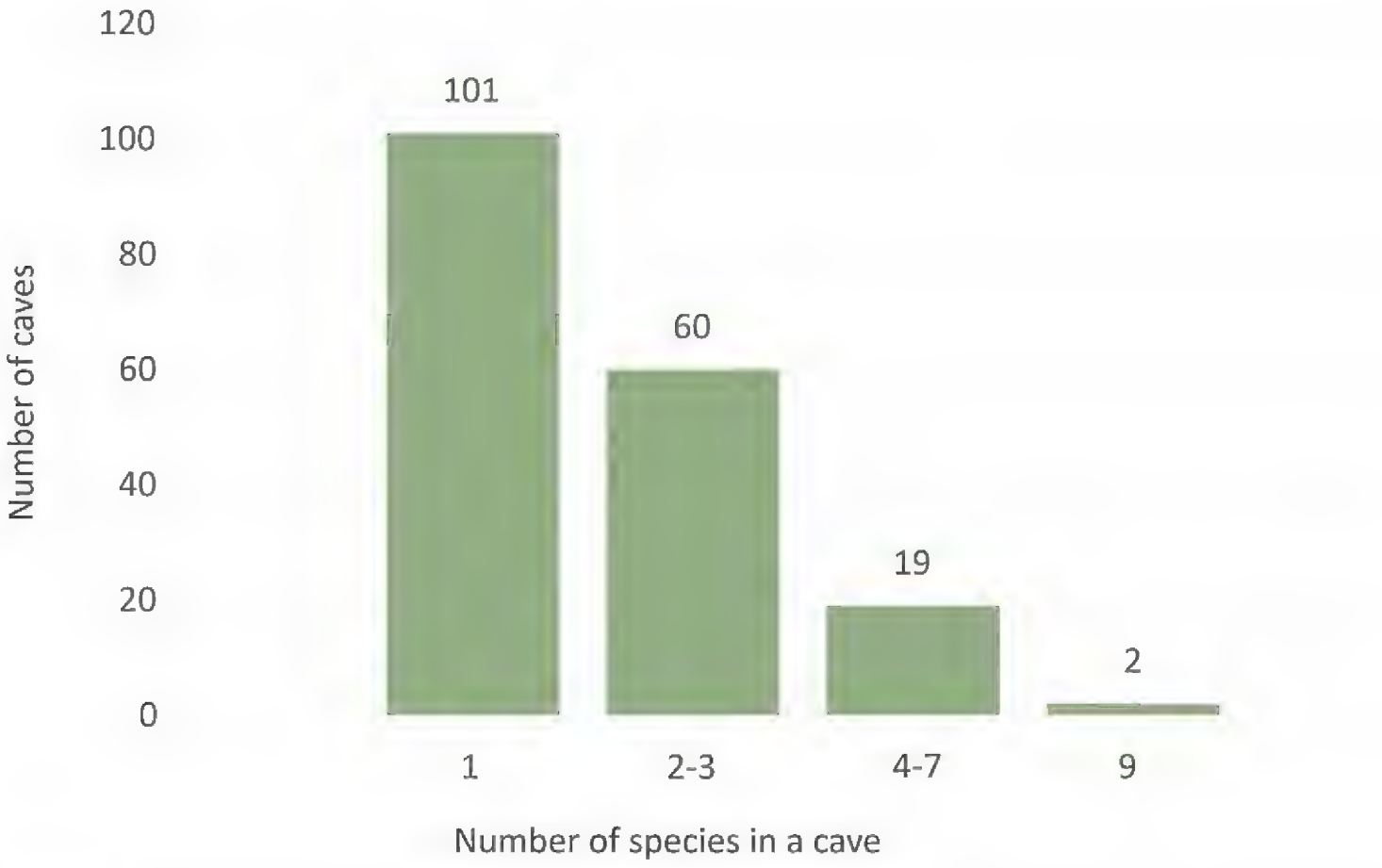

Figure 6. The number of caves in Greece that are reported to host from one to nine cave-dwelling gastropods.

Troglobionts and troglophiles comprise 14% and 40% of the cave-dwelling gastropod fauna respectively while 46% is characterized as trogloxene. Note that for a high proportion of taxa, the ecological classification cannot be made with certainty, regardless the chosen classification system (Sket 2004). For this reason, the reader should be cautious with these numbers. For example, many species classified as trogloxenes may have a variety of reasons penetrating caves such as seeking for more stable climatic conditions or—for the carnivorous species—searching for food (Weigand 2014). Most of the trogloxenes however, probably have an accidental presence in the caves. Many of these are not active visitors or by chance crawling in the caves but could have been washed into the cave by the rain. This is especially true for the species collected only as empty shells.

To date, more than 322 terrestrial gastropod species have been reported from subterranean habitats around the world, classified into 74 genera within 32 families (Grego 2022). The highest diversity of underground terrestrial gastropods is known from Europe (accounting for 59% of global taxa) and includes the Dinaric region (accounting for 25% of the global taxa) (Grego 2022). According to Sket et al. (2004), 49 species of obligate subterranean terrestrial gastropods have been reported from the Balkans. Thirty-six species are known from the western Balkans (Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Serbia, and North Macedonia) and 13 species from Greece (including the Aegean islands and Crete). Since then, more species have been described, e.g. at least seven species of the genus *Zospeum* [*Z. bucculentum*, *Z. clathratum*, *Z. manitaense*, *Z. pagodulum*, *Z. robustum and Z. simplex* all described by Inäbnit, Jochum & Neubert, 2019 in Inäbnit et al. (2019) and *Z. tholussum* Weigand, 2013 (Weigand 2013)].

It is difficult to compare the fauna of Greece with other countries, mainly the neighboring ones. One reason for this is that caves are generally underexplored (Wynne 2022). Even if a cave has been explored for its fauna, the data sometimes depend on the specialty of the researcher. For example, a bat specialist, will in general focus on bats and not on snails while a malacologist may not focus on or collect arthropods. Another reason is that the data is not easily accessible and there are not lists for every region and/or country. Finally, it is difficult to define the exact number of troglobiontic taxa of terrestrial gastropods, due to different definitions of the term "troglobiont", to inadequate knowledge of the morphology and biology of the taxa, and undefined taxonomic status (Gottstein 2002). Focusing on the Balkans, aggregated data are available for Bulgaria and Croatia. Although the latter is not a direct neighbour of Greece, it is worth mentioning because the karst areas in Croatia, are part of the Dinarides and most part of Greece, is an extension of them. The Dinarides, have been defined as a global hotspot for subterranean biodiversity (Gottstein 2002; Grego 2022; Lukić et al. 2023). In Croatia (56,600 km^2, more than 7,000 registered caves and potholes), although there has been no systematic research on terrestrial cave malacofauna, at least 19 troglobiont molluscan species have been recorded, seven of which are endemic to Croatia and one species common to Greece, *Pholeoteras euthrix* (Gottstein 2002). In total, two genera are common between the two countries (*Pholeoteras* and *Gyralina*).

On the other hand, Bulgaria (111,000 km^2, 5,000 caves and potholes) and Greece, two neighbouring countries that share the speleozoogeographic zones of Rhodopes (Georgiev 1977 in: Beron 2001), do not share any troglobiont species. According to Beron (2001), of the 20 terrestrial mollusc species reported from the 250 researched Bulgarian caves, none are considered troglobionts.

Of the 10,000 known caves of Greece, only 558 have been speleobiologically explored, while snails have been recorded in 182. Although speleobiologists have done a lot of work in the recent decades, there are still many more caves to be surveyed. The case of *Mediterranea amaltheae*, which was considered a single-cave endemic and in the present study was found in six more caves on the island of Crete, is evidence that the caves of Greece are undersuveyed. The new generation of speleobiologists in Greece, still have a broad field to explore. We believe that with the increasing exploration of Greek caves, the number of known species inhabiting caves will increase and new species will be discovered.

Acknowledgments

We would like to acknowledge all the collectors who, beside the authors, provided specimens studied in the present paper, namely Beron P., Butot, L.J.M., Georgiakakis P., Kontos P., Nikoloudakis G., Riedel A. and Subai P. The authors would like to thank Weigand A., Njunjić I., Grego J. and an anonymous reviewer for their suggestions and comments which improved the quality of the manuscript.

References

Alexiou S, Bakolitsas K, Russo C di, Latella L, Rampini M, Zacharias S (2014) Biospeleological notes on the caves of Parnassos, Giona and Vardousia mountains (Sterea Ellada). Parnassiana Archives 2: 71–81.

Arndt E, Subai P (2012) Gastropoda from subterranean habitats in Greece. Vernate 31: 213–224.

Bank RA, Menkhorst H (1988) Eine neue *Doraegopis*-Art von Euboea, Griechenland (Gastropoda Pulmonata: Zonitidae). Basteria 52: 147–150.

Bank RA, Menkhorst H (1992) Notizen zur Familie Enidae, 4. Revision der griechischen Arten der Gattungen *Ena*, *Zebrina*, *Napaeopsis* und *Turanena* (Gastropoda Pulmonata: Pupilloidea). Basteria 56(4/6): 105–158.

Bernasconi R, Riedel A (1994) Mollusca. In: Juberthie C, Decu V (Eds) Encyclopedia Biospeologica, 53–61.

Beron P (1985) On the cave fauna of the Greek islands of Sandorin and Iraklia, with preliminary description of a new pseudoscorpio. Grottes Bulgares 3: 64–71.

Beron P (2001) Étude comparative des faunes cavernicoles de la Bulgarie et de la Grece. Historia Naturalis Bulgarica 13: 53–68.

Beron P (2015) Cave Fauna of Bulgaria. National Museum of Natural History, Bulgarian Academy of Sciences (Eds) East-West Publishing, Sofia, 439 pp. https://doi.org/10.1007/978-1-4020-5781-6_17

Beron P (2016) Faune cavernicole de la Grèce. Maison d'édition Est-West: 1–229.

Beron P, Petrov BP, Stoev P (2004) The Invertebrate cave fauna of the Eastern Rhodopes (Bulgaria and Greece) Pages 791–822. In: Beron P, Popov A (2004) Biodiversity of Bulgaria. 2. Biodiversity of Eastern Rhodopes (Bulgaria and Greece). Pensoft Publishers.

Bonzano C, Calandri G (1984) Osservazioni biospeleologiche preliminari su alcune cavità della Grecia Occidentale. Ricerche sul carsismo della Grecia Occidentale. Ed. G.S. Imperiese, 75–84.

Born I von (1778) Index rerum naturalium Musei Caesarei Vindobonensis. Verzeichniss der Natürlichen Seltenheiten des K.K. Naturalien Kabinets zu Wien. Erster Theil, Schalthiere Pars 1 Testacea. https://doi.org/10.5962/bhl.title.11581

Böttger O (1882) Nacktschnecken aus Epirus und von den Jonischen Inseln. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 14: 96–101. https://www.biodiversitylibrary.org/page/31095866

Böttger O (1885) Aufzählung der in Thessalien gesammelten Gastropoden. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 12: 158–200.

Böttger O (1889) Verzeichnis der von Herrn E. von Oertzen aus Griechenland und aus Kleinasien mitgebrachten Vertreter der Landschneckengattung Clausilia Drap. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 16(1): 29–68. https://www.biodiversitylibrary.org/page/48489944

Bourguignat MJR (1856) Aménités malacologiques. Revue et Magasin de Zoologie pure et appliquée 8: 378–386.

Bourguignat MJR (1863–1868) Mollusques nouveaux, litigieux ou peu connus. Paris, 1–324.

Bruguière JG, Deshayes GP, Lamarck J-BPA de M de (1792) Histoire naturelle des vers. Chez Panckoucke, imprimeur-libraire, A Paris, 794 pp. https://doi.org/10.5962/bhl.title.49857

Chen Z, Auler AS, Bakalowicz M, Drew D, Griger F, Hartmann J, Jiang G, Moosdorf N, Richts A, Stevanovic Z, Veni G, Goldscheider N (2017) Le programme de la Carte Mondiale des Aquifères Karstiques: concept, procédure de cartographie et carte de l'Europe. Hydrogeology Journal 25: 771–785. https://doi.org/10.1007/s10040-016-1519-3

Da Costa EM (1778) Historia naturalis testaceorum Britanniæ, or, the British conchology; containing the descriptions and other particulars of natural history of the shells of Great Britain and Ireland: illustrated with figures. In English and French. London, 254 pp.

Damjanov SG, Pintér L (1969) Neue Vitreini aus Bulgarien (Gastropoda: Euthyneura). Archiv für Molluskenkunde 99(1/2): 35–40.

Di Russo C, Rampini M (2001) The Zoodochos cave in Santorini Island. Mémoires de Biospéologie 28: 201–202.

Di Russo C, Rampini M, Cobolli M (2014) Species delimitation: a problem in evolution and taxonomy View project Population genetics for fisheries and acquaculture View project. Biodiversity Journal 5: 397–420.

Draparnaud JPR (1801) Tableau des mollusques terrestres et fluviatiles de la France. Montpellier/Paris (Renaud/Bossange, Masson & Besson), 116 pp. https://doi.org/10.5962/bhl.title.40947

Draparnaud JPR (1805) Histoire naturelle des mollusques terrestres et fluviatiles de la France. Paris, 380 pp. https://doi.org/10.5962/bhl.title.12856

Erőss ZP, Fehér Z, Páll-Gergely B (2011) A new species of *Balcanodiscus* Riedel & Urbański, 1964 (Gastropoda: Pulmonata: Zonitidae) from northeastern Greece. Journal of Conchology 40: 577–581.

Fehér Z, Szekeres M (2016) Taxonomic revision of the rock-dwelling door snail genus *Montenegrina* Boettger, 1877 (Mollusca, Gastropoda, Clausiliidae). ZooKeys 599: 1–137. https://doi.org/10.3897/zookeys.599.8168

Férussac A (1821) Tableaux systematiques des animaux mollusques classes en familles naturelles: dans les quels on a établi la concordance de tous les systèmes; suivis d'un Prodrome général de tous les mollusques terrestres ou fluviatiles vivants ou fossiles. Paris.

Férussac A (1932) 1819–1851. Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles, tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles. Tome premier. In: Paris, 422 pp. https://doi.org/10.5962/bhl.title.124603

Forcart L (1950) Systématique des mollusques en forme de *Daudebardia* et révision des espèces d'Anatolie et de l'ile de Crête. Journal de Conchyliologie 90(2): 107–117.

Frank C (1988) Über Molluskenfunde von den Inseln Chios, Kreta und Zypern sowie vom griechischen Festland (Thessalien). Bericht des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck, 1–11.

Fuchs A, Käufel F (1936) Anatomische und systematische Untersuchungen and Land- und Süßwasserschnecken aus Griechenland und von den Inseln des Ägäischen Meeres. Archiv für Naturgeschichte, Neue Folge 5: 541–662.

Gasparo F (2009) La Grotta di Zoodochos Pigi a Santorini (Cicladi, Grecia) e la sua fauna. Progressione 55: 102–105.

Georgiev D (2016) *Vitrea neglecta* Damjanov et L. Pintér 1969 - genital anatomy of a specimen from Greece. ZooNotes 95: 95–97.

Gittenberger E (1977) Cave snails from Corfu, Greece. Comunicacions del Simposium d'Espeleologia (Bioespeleologia) 6: 47–53.

Gittenberger E (1985) Beiträge zur Kenntnis der Pupillacea. XI. *Speleodentorcula beroni* Gen. & Spec. Nov. (Mollusca: Gastropoda: Orculidae) aus einer Höhle in Euboea, Griechenland. Zoologische Mededelingen 59(19): 221–228.

Gittenberger E (1986) Zoogeographical notes concerning the terrestrial mollusca of the Ionian islands Kerkyra, Lefkas and Kephallinia. Biologia Gallo-Hellenica 12: 363–370.

Gittenberger E (2000) Serrulininae in Greece, there may be more (Gastropoda, Pulmonata, Clausiliidae). Basteria 64(4/6): 81–87.

Gittenberger E, Hausdorf B (2004) The *Orculella* species of the South Aegean island arc, a neglected radiation (Gastropoda, Pulmonata, Orculidae). Basteria 68: 93–124.

Gottstein S, Bakran-Petricioli T, Bedek J, Bukovec D, Buzjak S, Franičević M, Jalžić B, Kerovec M, Kletečki E, Kralj J, Kružić P, Kučinić M, Kuhta M, Matočec N, Ozimec R, Rada T, Štamol V, Ternjej I, Tvrtković N (2002) An overview of the cave and interstitial biota of Croatia. Natura Croatica 11(Suppl): 1–112.

Guéorguiev VB (1977) La faune troglobie terrestre de la péninsule Balkanique. Origine, formation et zoogéographie. Editions de l' Academie Bulgare des Sciences, 182 pp.

Grego J (2022) Biology and Ecology of Subterranean Mollusca. Pages 95–163. In: Wynne JJ (Ed.) Cave biodiversity: speciation and diversity of subterranean fauna. Johns Hopkins University Press, 352 pp.

Guéorguiev VB (1977) La faune troglobie terrestre de la péninsule Balkanique. Origine, formation et zoogéographie. Editions de l' Academie Bulgare des Sciences, 182 pp.

Hausdorf B (1996) Die Orculidae Asiens (Gastropoda: Stylommatophora). Archiv für Molluskenkunde 125: 1–86. https://doi.org/10.1127/arch.moll/125/1996/1

Hausdorf B, Sauer J (2009) Revision of the Helicellinae of Crete (Gastropoda: Hygromiidae). Zoological Journal of the Linnean Society 157(2): 373–419. https://doi.org/10.1111/j.1096-3642.2008.00504.x

Hesse P (1882) Eine Reise nach Griechenland. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 9(4): 283–336. https://www.biodiversitylibrary.org/page/16360076.

Inäbnit T, Jochum A, Kampschulte M, Martels G, Ruthensteiner B, Slapnik R, Nesselhauf C, Neubert E (2019) An integrative taxonomic study reveals carychiid microsnails of the troglobitic genus *Zospeum* in the Eastern and Dinaric Alps (Gastropoda, Ellobioidea, Carychiinae). Organisms Diversity & Evolution. 19(2): 135–177. https://doi.org/10.1007/s13127-019-00400-8

IUCN (2023) The IUCN Red List of Threatened Species. Version 2022–2. https://www.iucnredlist.org [accessed 24/11/2023]

Käufel F (1930) Zoologische Forschungsreise nach den Jonischen Inseln und dem Peloponnes. X. Teil. Die schalentragenden Land- und Süßwassermollusken. Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-naturwissenschaftliche Klasse, Abteilung I.

Klemm W (1962) Zoologische Studien in West-Griechenland. X. Teil. Die Gehäuseschnecken. Sitzungsberichte der Österreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung 1.

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata [10th revised edn.], Laurentius Salvius: Holmiae, Vol. 1, 824 pp. https://doi.org/10.5962/bhl.title.542

Linnaeus C (1767) Systema Naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. 1 & 2. Holmiae [Stockholm], Laurentii Salvii, 533 pp. https://doi.org/10.5962/bhl.title.157601

Lukić M, Fišer C, Delić T, Bilandžija H, Pavlek M, Komerički A, Dražina T, Jalžić B, Ozimec R, Slapnik R, Bedek J (2023) Subterranean Fauna of the Lukina Jama–Trojama Cave System in Croatia: The Deepest Cave in the Dinaric Karst. Diversity 15: 726. https://doi.org/10.3390/d15060726

Maassen WJM, Riedel A (1991) Über eine Zwergrasse von *Oxychilus* (*Schistophallus*) *minoicus* Riedel (Gastropoda Pulmonata: Zonitidae). Basteria. 55: 177–183.

Maassen WJM (1995) Observations on the genus *Mastus* from Crete (Greece), with descriptions of twelve new species (Gastropoda Pulmonata: Buliminidae). Basteria 59: 31–64.

Maltzan H von (1884) Beitrag zur Kenntnis einiger osteuropäischer Heliceen. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 16(5): 1–75. https://www.biodiversitylibrary.org/page/30957904

Maltzan H von (1887) Neue kretenser Landschnecken. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 14: 117–119. https://www.biodiversitylibrary.org/page/15886613

Martens E von (1889) Griechische Mollusken. Gesammelt von Eberh. von Örtzen. Archiv für Naturgeschichte 55: 169–240.

Menke KT (1828) Synopsis methodica molluscorum generum omnium et specierum earum, quae in Museo Menkeano adservantur; cum synonymia critica et novarum specierum diagnosibus. Pyrmonti, 1828, 1–116. https://doi.org/10.5962/bhl.title.13182

MolluscaBase [Eds] (2023) MolluscaBase. https://www.molluscabase.org [accessed 24/11/2023]

Mousson A (1854) Coquilles terrestres et fluviatiles recueillies par M. le Prof. Bellardi dans un voyage en Orient. https://doi.org/10.5962/bhl.title.101714

Mousson A (1859) Coquilles terrestres et fluviatiles, recueillies dans l'Orient par M. le Dr. Alex. Schläfli. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 4(3): 253–297. https://doi.org/10.5962/bhl.title.101882

Müller OF (1774) Vermium terrestrium et fluviatilium, seu animalium infusorium, Helminthicorum, et testaceorum, non marinorum, succincta historia 2, 1–214. https://doi.org/10.5962/bhl.title.12733

Nordsieck H (1972) Zur Anatomie und Sytematik der Clausilien, XI. Neue Formen und taxonomische Revision einiger Gruppen der Alopiinae. Archiv für Molluskenkunde. https://www.molluscabase.org/aphia.php?p=sourcedetails&id=296361

Olivier GA (1801) Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du Gouvernement, pendant les six premières années de la République. Paris, 432 pp. https://gdz.sub.uni-goettingen.de/id/PPN625322428

Paget O (1976) Die Molluskenfauna der Insel Rhodos. Annalen des Naturhistorischen Museums in Wien 80: 681–780.

Paragamian K, Nikoloudakis I, Papadatou E, Sfakianaki E (2004) Biological and Environmental Study of the Cave of Maroneia: Analysis of current status - Proposals., 176 pp.

Paragamian K, Paragkamian S (2023) Cave fauna of Greece database analysis (CFG Analysis) - Hellenic Institute of Speleological Research. https://inspee-hisr.github.io/CFG_analysis/ [accessed 22/8/2023]

Paragamian K, Poulinakis M, Paragkamian S, Nikoloudakis I (2023) Cave fauna of Greece database - Hellenic Institute of Speleological Research. https://database.inspee.gr/ [accessed 24/11/2023]

Pfeffer G (1930) Die Unterfamilie Zonitidae (Moll., Pulm.). Mitteilungen des Zoologischen Museums Berlin 16: 411–508.

Pfeiffer L (1846) Symbolae ad historiam Heliceorum. Sectio tertia. https://biodiversitylibrary.org/page/12254325

Pfeiffer L (1847) Diagnosen neuer Heliceen. Zeitschrift für Malakozoologie. Cassel. https://www.biodiversitylibrary.org/page/16292006

Pfeiffer L (1849) Nachträge zu L. Pfeiffer Monographia Heliceorum. Zeitschrift für Malakozoologie. Cassel (Theodor Fischer). https://biodiversitylibrary.org/page/16300164

Pfeiffer L (1853) Monographia heliceorum viventium. Sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen tertium [Vol. 3]. Lipsiae: Brockhaus. [i–viii +] 711 pp. https://biodiversitylibrary.org/page/11646394

Pfeiffer L (1854) Descriptions of fifty-seven new species of Helicea, from Mr. Cuming's collection. In: Proceedings of the Zoological Society of London, 286–298. https://doi.org/10.1111/j.1469-7998.1854.tb07277.x

Pfeiffer L (1856) Bericht über weitere Mittheilungen des Herrn Zelebor. Malakozoologische Blätter. Cassel (Theodor Fischer). https://www.biodiversitylibrary.org/page/15865142

Pintér L (1972) Die Gattung *Vitrea* Fitzinger, 1833 in den Balkanländern (Gastropoda: Zonitidae). Annales Zoologici 29(8): 209–315.

Pintér L (1983) Zwei neue *Vitrea*-Arten (Gastropoda: Zonitidae). Acta Zoologica Academiae Scientiarum Hungaricae 29: 219–222.

Pintér L, Riedel A (1983) Über eine neue *Lindbergia*-Art von Kérkyra, Griechenland (Gastropoda: Zonitidae). Zoologische Mededelingen 57(11): 101–103.

Potiez VLV, Michaud ALG (1838) Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai. Tome 1, xxxvi + 560 + 4 (Relevé des genres manquants; Errata). Atlas, pp. 1–56, pls I–XXXVII [= 1–37]. Paris: Baillière. https://www.biodiversitylibrary.org/page/10934167

Reeve LA (1849) Monograph of the genus *Bulimus*. Conchologia Iconica, or, Illustrations Of The Shells Of Molluscous Animals 5: 1–89. https://doi.org/10.5962/bhl.title.125468

Reinhardt O (1871) Über die in Deutschland vorkommenden Hyalinen aus der Crystallina-Gruppe. Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin: 33–41.

Reischütz A, Reischütz PL (2003) Helleniká pantoía, 3: Die Schönste von allen. *Tsoukatosia* (*Agiosspeleikos*) *christinae* nov. subgen., nov. spec. (Clausiliidae: Pulmonata: Gastropoda). Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 11: 1–3.

Reischütz A, Reischütz PL, Szekeres M (2016) The Clausiliidae subfamily Phaedusinae (Gastropoda, Pulmonata) in the Balkans. Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 23: 93–117.

Reischütz A, Steiner-Reischütz N, Reischütz PL (2017) Helleniká pantoía, XLVI. Die Messa Mani (Peloponnes, Griechenland)-35 Jahre später. Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 24: 63–64.

Reischütz A, Steiner-Reischütz N, Reischütz PL (2020) Helleniká pantoía, LX. Zur Typuslokalität von *Tsoukatosia christinae* A. Reischütz & P. L. Reischütz 2003 (Clausiliidae: Pulmonata: Gastropoda) auf der Peloponnes (Griechenland). Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 27: 53–56.

Reischütz PL (1986) Die Gattung *Balcanodiscus* Riedel & Urbański, 1964 in Griechenland (Gastropoda, Stylommatophora, Zonitidae). Mitteilungen der Zoologischen Gesellschaft Braunau 4(14): 349–351.

Reischütz PL (1988) Beiträge zur Molluskenfauna Thrakiens und Ostmakedoniens, II. Annalen des Naturhistorischen Museums in Wien 341–356.

Riedel A (1958) Über *Oxychilus samius* (Martens, 1889) (Gastropoda, Zonitidae). Mitteilungen aus dem Zoologischen Museum in Berlin 34: 109–111. https://doi.org/10.1002/mmnz.19580340106

Riedel A (1959) Die von Dr. K. Lindberg in Griechenland gesammelten Zonitidae (Gastropoda). Annales Zoologici 18(6): 89–117.

Riedel A (1960) Die Gattung *Lindbergia* Riedel (Gastropoda, Zonitidae) nebst Angaben über *Vitrea illyrica* (A. J. Wagner). Annales Zoologici 18: 333–346.

Riedel A (1962) Materialien zur Kenntnis der paläarktischen Zonitidae (Gastropoda). VII–VIII. Annales Zoologici 20: 221–227.

Riedel A (1968) Zonitidae (Gastropoda) Kretas. Annales Zoologici 25: 473–537.

Riedel A (1969) Die Ägäis - und die Verbreitung der Zonitidae (Gastropoda) in der östlichen Mittelmeerländern. Annales Zoologici 27: 29–51.

Riedel A (1972) Die Untergattung *Schistophallus* A.J. Wagner in Europa und Kleinasien (Gastropoda, Zonitidae). Annales Zoologici 29(7): 181–207.

Riedel A (1977) Materialen zur Kenntnis der Zonitidae (Gastropoda). IX–XI. Annales Zoologici 33(24): 495–515.

Riedel A (1978) Kritische Bemerkungen und Ergänzungen zur Kenntnis der Subfamilie Daudebardiinae (Gastropoda, Zonitidae) mit Verzeichnis aller akzeptierten Arten. Annales Zoologici 24(8): 139–206.

Riedel A (1979) Materialen zur Kenntnis der paläarktischen Zonitidae (Gastropoda). XII–XIV. Annales Zoologici 35: 115–125. https://doi.org/10.3161/00159301FF1979.25.9.115

Riedel A (1981a) Eine neue unterirdische *Lindbergia*-Art von der Insel Kasos, Griechenland (Gastropoda, Zonitidae). Annales Zoologici 36: 282–287.

Riedel A (1981b) Vitreini (Gastropoda, Zonitidae) von den ägäischen Inseln Chios, Samos und Ikaria. Annales Zoologici 36(11): 229–240.

Riedel A (1982) Die Gattungen *Allaegopis* Riedel und *Doraegopis* gen. n. (Gastropoda, Stylommatophora, Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 8(1): 1–28.

Riedel A (1983) Manche wenig bekannte und neue *Oxychilus*-Arten aus Griechenland (Gastropoda, Zonitidae). Annales Zoologici 37(7): 269–288.

Riedel A (1984) Eine neue *Lindbergia*-Art von der Insel Thira, Griechenland (Gastropoda, Stylommatophora, Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 10(1): 1–4.

Riedel A (1985a) Revision der Gattung *Zonites* Montfort (Gastropoda: Zonitidae): griechische Arten. Annales Zoologici 39(1): 1–67.

Riedel A (1985b) Zur Kenntnis der Gattung *Balcanodiscus* (Gastropoda, Stylommatophora, Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 10: 139–146.

Riedel A (1986) Eine neue *Allaegopis*-Art aus dem Peloponnes Gastropoda, Stylommatophora, Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 11(8): 87–92.

Riedel A (1988a) Die Gattung *Carpathica* A.J. Wagner in Griechenland (Gastropoda, Stylommatophora, Daudebardiidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 13: 85–92.

Riedel A (1988b) Zur Kenntnis der Gattung *Balcanodiscus*, II (Gastropoda, Stylommatophora, Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 13: 93–104.

Riedel A (1990) Neue und wenig bekannte Zonitidae (Gastropoda) aus Griechenland. Annales Zoologici 43(25): 493–534.

Riedel A (1992) Fauna Graeciae V. The Zonitidae (sensu lato) (Gastropoda, Pulmonata) of Greece. Hellenic Zoological Society 8: 194.

Riedel A (1993) Différenciation et distribution géographique des Zonitidae (Gastropodes Terrestres) en Grèce. Biologia Gallo-Hellenica 20: 31–43.

Riedel A (1995) Zur Kenntnis der griechischen und türkischen Zonitidae nebst Beschreibung von drei neuen Arten (Gastropoda; Stylommatophora). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 17: 137–150.

Riedel A (1996) Die in West-Paläarktis unterirdisch lebenden Zonitidae sensu lato (Gastropoda, Stylommatophora). Fragmenta Faunistica 39(24): 363–390. https://doi.org/10.3161/00159301FF1996.39.24.363

Riedel A (1999) Zwei neue *Oxychilus*-Arten von Südanatolien und von den Ägäischen Inseln (Gastropoda: Stylommatophora: Zonitidae). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 19: 217–223.

Riedel A, Subai P (1978) Eine neue *Oxychilus*-Art (Gastropoda, Zonitidae) von den Ionischen Inseln. Annales Zoologici 34(4): 79–84.

Riedel A, Subai P (1982) Beschreibung einer neuen *Oxychilus* Art aus Kreta nebst neuen Angaben über *Oxychilus ionicus* (Gastropoda, Zonitidae). Archiv für Molluskenkunde 112: 21–26.

Riedel A, Subai P (1993) Über *Gyralina* und *Spelaeopatula* nebst Beschreibung neuer Taxa (Gastropoda Pulmonata: Zonitidae). Archiv für Molluskenkunde 121: 53–66. https://doi.org/10.1127/arch.moll/121/1992/53

Rossmässler EA (1835–1844) Iconographie der Land- & Süßwasser- Mollusken, mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten., 132 pp.

Roth JR (1839) Molluscorum species, quas in itinere per Orientem facto comites clariss. Schubert doctores M. Erdl et J.R. Roth collegerunt. Dissertatio Inauguralis, 34 pp. https://doi.org/10.5962/bhl.title.10692

Roth JR (1855) Spicilegium molluscorum orientalium annis 1852 et 1853 collectorum. Malakozoologische Blätter 2(8): 17–58.

Seidl F (1978) Zur Molluskenfauna von Kreta: Historische Aufzeichnungen, Aus dem Reisetagebuch von Hofrat Dr. Rudolf Sturany. Mitteilungen der Zoologischen Gesellschaft Braunau 3: 157–193.

Simroth H (1884) Ueber die deutschen und einge ausserdeutsche europäische Nacktschnecken. Vorläufige Mittheilung. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft. https://www.biodiversitylibrary.org/page/30957845

Simroth H (1889) Die von Herrn E. von Oertzen in Griechenland gesammelten Nacktschnecken. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 16(1): 3–27.

Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42 (21–22): 1549–1563. https://doi.org/10.1080/00222930801995762

Sket B (2016) Subterranean (Hypogean) Habitats in Karst and Their Fauna. In: The Wetland Book. Springer Netherlands, 14 pp. https://doi.org/10.1007/978-94-007-6173-5_241-1

Štamol V, Jalžić B, Kletečki E (1999) A contribution to knowledge about the distribution of the troglobiontic snail *Pholeoteras euthrix* Sturany, 1904 (Mollusca, Gastropoda). Natura Croatica 8: 407–419.

Sterki V (1880) *Hyalina depressa* n. sp. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 12: 104–105. https://www.biodiversitylibrary.org/page/30976053

Sturany R (1904) Ueber einige von Herrn G. Paganetti-Hummler entdeckte Höhlenschnecken. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 36(3): 103–107. https://www.biodiversitylibrary.org/page/15607970

Stussiner J, Böttger O (1885) Malakologische Ergebnisse auf Streifzügen in Thessalien. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 13: 42–73. https://www.biodiversitylibrary.org/page/16361665

Subai P (1993) Neue Arten seltener Landschnecken aus Griechenland und aus der Türkei (Gastropoda: Prosobranchia: Cyclophoridae; Pulmonata: Pupillidae, Clausiliidae). Archiv für Molluskenkunde 122: 63–69. https://doi.org/10.1127/arch.moll/122/1993/63

Subai P, Neubert E (2014) Revision of the genus *Lindholmiola* Hesse, 1931. Contributions to Natural History 23: 1–94.

Trajano E, de Carvalho MR (2017) Towards a biologically meaningful classification of subterranean organisms: A critical analysis of the schiner-racovitza system from a historical perspective, difficulties of its application and implications for conservation. Subterranean Biology 22: 1–26. https://doi.org/10.3897/subtbiol.22.9759

Urbański J (1960) Ein Beitrag zur Kenntnis der Molluskenfauna der Insel Thasos und des mazedonisch-thrazischen Küstenlandes. Izvestiya na Zoologicheskiya Institut Bulgarska Akademiya na Naukite 9: 71–105.

Vardinoyannis K, Parmakelis A, Triantis KA, Giokas S (2018) Land Molluscs in Greece: The Rich, Unique, Diverse, and Unprotected Animal Models. In: Sfenthourakis S, Pafilis P, Parmakelis A, Poulakakis N, Triantis K (Eds) Biogeography and biodiversity of the Aegean. In honour of Prof. Moysis Mylonas. Broken Hill Publishers Ltd, Nicosia, Cyprus, 47–66.

Wagner AJ (1928) Studien zur Molluskenfauna der Balkanhalbinsel mit besonderer Berücksichtigung Bulgariens und Thraziens, nebst monographischer Bearbeitung einzelner Gruppen. Prace Zoologiczne Polskiego Panstwowego Muzeum Przyrodniczego [Annales Zoologici Musei Polonici Historiae Naturalis].

Weigand AM (2013) New *Zospeum* species (Gastropoda, Ellobioidea, Carychiidae) from 980 m depth in the Lukina Jama–Trojama cave system (Velebit Mts., Croatia). Subterranean Biology. 11: 45–53. https://doi.org/10.3897/subtbiol.11.5966

Weigand AM (2014) Next stop: underground. Variable degrees and variety of reasons for cave penetration in terrestrial gastropods. Acta Carsologica 43(1): 175–183. https://doi.org/10.3986/ac.v43i1.585

Westerlund CA (1871) Fauna molluscorum terrestrium et fluviatilium Sveciae, Norvegiae et Daniae. I. Landmolluskerna. Adolf Bonnier, Stockholm, 1–296.

Westerlund CA (1892) Spicilegium Malacologicum. Neue Binnenconchylien in der paläarktischen Region. I, II. Verhandlungen der Kaiserlich-königlichen Zoologisch-botanischen Gesellschaft in Wien.

Wiktor A (1975) New slug species (Pulmonata: Milacidae and Limacidae) from the Balkan Peninsula. Annales Zoologici 33(6): 77–91.
Wolf B (1938) 3 Animalium Cavernarum Catalogus - Animalium Catalogus. Junk Verl. Wien, 918 pp.
Wynne JJ [Ed.] (2022) Cave biodiversity: speciation and diversity of subterranean fauna. Johns Hopkins University Press, 352 pp.

Supplementary material 1

List of caves and their locality. Caves with an asterisk (*) are artificial caves.
Authors: Danae Karakasi
Data type: xlsx
Explanation note: The table contains all caves mentioned in the text with detailed geographic information.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/subtbiol.48.113383.suppl1